JOURNAL

FISHERIES RESEARCH BOARD
OF CANADA

Volume [illegible], No. 11

CONTENTS

[illegible], A. J. [illegible] changes in the [illegible] of waters [illegible] the [illegible]
[illegible] Bay, New Brunswick [illegible]
[illegible] ecological aspects of the [illegible]
[illegible] phytoplankton [illegible]
[illegible] the [illegible], *Gadus morhua* L. [illegible]
[illegible] pink salmon [illegible] during early [illegible] Coast [illegible]
[illegible] FOLEY, H. F. [illegible]
[illegible] and [illegible]
[illegible] aspects of fish growth [illegible]

NOTES

[illegible] Strait of Georgia during July [illegible]
[illegible] By R. E. [illegible]
[illegible] By J. R. VALLENTYNE [illegible]
[illegible] Newfoundland [illegible] By [illegible] C. MERCER [illegible]
[illegible] By J. L. HART [illegible]
[illegible] depths. By F. A. [illegible]
[illegible]

[illegible] Research Board of Canada [illegible]

JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

Submissions for publication in the *Journal of the Fisheries Research Board of Canada* should concern aquatic organisms or environments that are relevant to Canada. They may be either original research articles or reviews, in English or in French. Articles are accepted without limitations as to origin, but must not have been published elsewhere or copyrighted. Opinions expressed by authors do not necessarily reflect those of the Board or policies of the Ministry of Fisheries of Canada.

A guide to contributors is included at the back of each *Journal* issue.

The publication of the *Journal*, together with its predecessors, has been continuous since 1901. Its predecessors are *Contributions to Canadian Biology* published from 1901 to 1922, *Contributions to Canadian Biology and Fisheries* from 1924 to 1934, and the *Journal of the Biological Board of Canada* from 1934 to 1937.

This *Journal* is published in annual volumes of twelve issues. This issue (Vol. 24, No. 11) was published November 10, 1967.

Editor:

J. C. STEVENSON

Associate Editor: G. I. PRITCHARD
Assistant Editor: R. H. WIGMORE

Production: R. L. MacIntyre

Fisheries Research Board of Canada
Office of the Editor
116 Lisgar Street
Ottawa 4, Ont., Canada

Manuscripts for publication should be addressed to the Editor

---

All Fisheries Research Board of Canada publications are for sale by the Queen's Printer, Ottawa. Remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. Subscription rates to the *Journal* are: Canada, United States, Mexico, $9.00, single issues $1.00; to other countries, $9.75 and $1.25.

The Fisheries Research Board of Canada also publishes a *Bulletin* series (issued irregularly), an *Annual Report*, and a biennial *Review of Investigations*. All publications may be consulted at Board establishments located at Ottawa, Nanaimo and Vancouver, B.C.; Winnipeg, Man.; Ste. Anne de Bellevue and Grande-Rivière, Que.; St. Andrews, N.B.; Halifax and Dartmouth, N.S.; Ellerslie, P.E.I.; and St. John's, Nfld.

Annual Changes in the Oceanic-Coastal Waters of the Eastern Subarctic Pacific[1,2]

By A. J. Dodimead

Fisheries Research Board of Canada
Pacific Oceanographic Group, Nanaimo, B.C.

and G. L. Pickard

Institute of Oceanography, University of British Columbia
Vancouver, B.C.

ABSTRACT

The temporal variations of water characteristics and currents are reviewed both for the oceanic region of the eastern Subarctic Pacific and for the bordering coastal and fjord regions.

In the oceanic region, an estuarine structure prevails, namely, an upper zone, halocline, and lower zone. The horizontal distributions of temperature of the upper zone (seasonal) for the years 1955 to 1966, and lower zone waters for the same years, excepting 1963 and 1964, off the British Columbia coast are presented. The extent of warm upper-zone waters was greatest in 1958 and 1963 and least in 1956 and 1965. Warm lower-zone waters extended furthest in 1958, 1961, and 1962, but did not retreat to the position observed in 1956. The mechanisms relating these waters to the bottom waters of the continental shelf are discussed.

In the coastal and the inshore waters there is a pronounced annual cycle in the upper zone, generally with a temperature maximum and a salinity maximum in the summer. The deep water of the fjords opening directly on the Pacific is, in some cases, exchanged annually in the summer, when higher density subsurface water moves onto the continental shelf. In the fjords with indirect connection to the ocean, the deep water is exchanged irregularly at intervals of several years.

INTRODUCTION

This report is a summary of the principal oceanographic features, mechanisms, and temporal changes in the oceanic-coastal waters of the eastern Subarctic Pacific (Fig. 1).

OCEANIC WATERS

The salinity and temperature structures, circulation, and temporal variability in the Subarctic Pacific have recently been reviewed by Uda (1963), Dodimead et al. (1963), and Tabata (MS, 1964). This section presents a summary of some of these features, data for 1955 and 1956 showing the extent of warmwater intrusions off the British Columbia coast, and the relation of the intrusions to the bottom waters of the Continental Shelf.

---

[1] Received for publication June 14, 1967.

[2] Presented in essentially the same form at the Eleventh Pacific Science Congress, Tokyo, Japan, 1966.

J. Fish. Res. Bd. Canada, 24(11), 1967.
Printed in Canada.

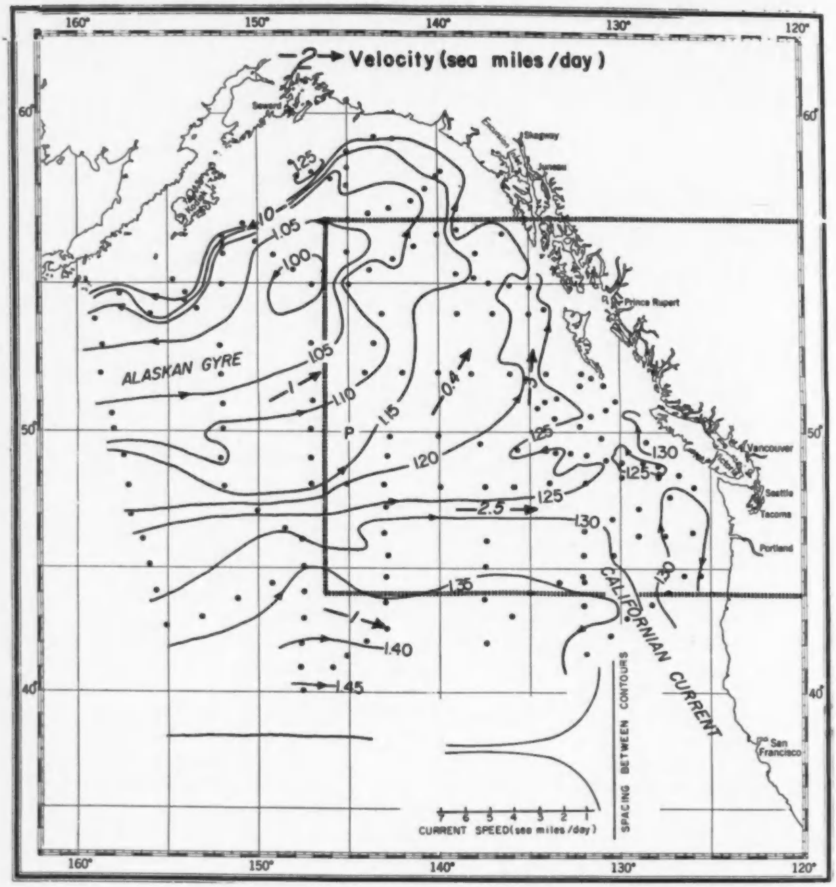

160°
150°
140°
130°
120°
60°
50°
40°
2
Velocity (sea miles/day)
Seward
Skagway
Juneau
Prince Rupert
Vancouver
Victoria
Seattle
Tacoma
Portland
San Francisco
ALASKAN GYRE
CALIFORNIAN CURRENT
P
1.25
1.10
1.05
1.00
1.05
1
1.10
1.15
0.4
3
1.20
1.25
1.30
1.25
2.5
1.25
1.30
1.30
1.35
1
1.40
1.45
7 6 5 4 3 2 1
CURRENT SPEED (sea miles/day)
SPACING BETWEEN CONTOURS

FIG. 1. Geopotential topography, 0/1000 decibars, eastern Subarctic Pacific, June 1962 (broken line encompasses area shown in subsequent figures).

1. GEOSTROPHIC CIRCULATION

The general circulation consists of an eastward flow, which divides near the coast; part goes south to form the California Current, and part turns northward into the Gulf of Alaska (Fig. 1). The northward flow between the coast and Ocean Station P is relatively slow, varying from 2 to 5 miles per day, and is usually characterized by meanders and eddies. Similar features occur at other depths, but the velocities are less.

2. SALINITY AND TEMPERATURE STRUCTURES

The oceanic waters have a unique and permanent salinity structure, namely: (1) an upper zone (seasonal) from 0 to about 100 m depth; (2) a halocline in which the salinity increases by about 1‰ in the depth interval from about 100 to 200 m; and (3) a lower zone (non-seasonal) in which the salinity increases gradually with depth (Fig. 2). It is a typical estuarine structure due to excess of precipitation and runoff over evaporation.

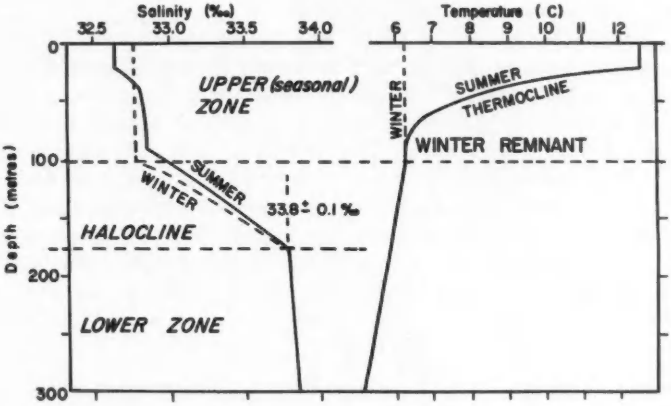


FIG. 2. Salinity and temperature structures in the eastern Subarctic Pacific.

On the other hand, the temperature structure varies markedly with the seasons. A well-developed thermocline prevails in the upper zone in summer but is absent in winter, when the waters are isothermal and isohaline to the top of the halocline (Fig. 2). The annual range of temperature of the surface water is about 6–8 C.

Mechanisms for the formation of these structures, and the significance of these zones and their points of discontinuity, have been proposed by Doe (1955), Fleming (1958), Tully and Barber (1960), Dodimead (1961), and Tully and Giovando (1963). Conclusions significant to this section are:

(*a*) The temperature at the top of the halocline in summer is approximately that which the water had when it was part of a homogeneous layer the previous winter. Salinities at this level are about 0.2‰ higher in summer than in winter (Dodimead, 1961).

(*b*) Horizontal temperature distributions at the top of the halocline during summer are similar to those of the previous late winter and hence are similar to winter surface distributions of minimum temperatures (Dodimead, 1961).

(*c*) The bottom of the halocline is that level at which the transfer of seawater is uni-directional upward. Therefore, the lower limit of the halocline is below the surface effects such as cooling, heating, and evaporation (Tully and Barber, 1960).

(*d*) The bottom of the halocline can be defined by the isohaline surface of salinity = 33.8‰ ± 0.1‰ (Doe, 1955; Dodimead, 1958; Fleming, 1958).

(*e*) Temperatures of water at 33.8‰ provide single-valued, numerical indices of the non-seasonal waters (Tully and Barber, 1960).

(*f*) Temperature distributions on the 33.8‰ surface coincide in every principal feature with temperature distributions on isopycnal surfaces near this level (Tully and Barber, 1960).

From these conclusions it follows that:

(*a*) Much information on the annual variations of temperature in the seasonal and non-seasonal waters can be obtained from horizontal distributions at the top of the halocline and on the 33.8‰ surfaces, respectively.

(*b*) A steady state condition appears to exist at these levels from late winter through until late summer. Consequently, annual changes in the horizontal distributions occur predominantly during the autumn and early winter months. Thus, synoptic data for different years need not be taken in the same time period for comparative purposes, providing they are taken during the relatively steady-state period. Further, late winter surface temperatures or minimum temperatures from bathythermograms taken in summer can be used in lieu of serial observations of temperature and salinity to define the temperature at the top of the halocline.

3. DEPTH OF TOP OF HALOCLINE AND OF 33.8‰ SALINITY SURFACE

The depth of the top of the halocline decreases shoreward, from about 100 m at 200 miles from the coast to 60 m near the coast (Fig. 3A). The shallowest depths are associated with the low-salinity waters.

The depth of the 33.8‰ salinity surface is of the order of 180 m (Fig. 3B).

4. TEMPERATURE DISTRIBUTIONS AT THE TOP OF THE HALOCLINE

The distributions for 1955–58 shown in Fig. 4 were prepared from serial oceanographic data taken in midsummer synoptic cruises. The shaded water has temperatures greater than 7 C. Waters at the top of the halocline were warmest during 1958 and coldest during 1956 in these 4 years.

The charts in Fig. 5 were prepared from midsummer data for 1959 and 1960, and from early summer data for 1961 and 1962. The distribution of the 7-degree water was fairly extensive during these 4 years; the westward extent off the British Columbia coast was less than observed during 1958 but greater than observed in 1955 through 1957.

For the years 1963–66, only surface temperature and bathythermograph data were available. The distributions of waters of temperatures greater than 7 C for 1963 and 1964, as interpolated from March surface temperature charts issued by the Bureau of Commercial Fisheries, La Jolla, and of minimum winter temperatures, as interpreted from bathythermograms for 1965 and 1966, are shown in Fig. 6. Of these years 1965 was the coldest. The extent of the 7-degree water was largest in 1963.

5. TEMPERATURE DISTRIBUTIONS ON THE 33.8‰ SALINITY SURFACE

In Fig. 7, 8, and 9, waters having temperatures greater than 6.5 C are shaded. These temperature distributions of the non-seasonal waters show

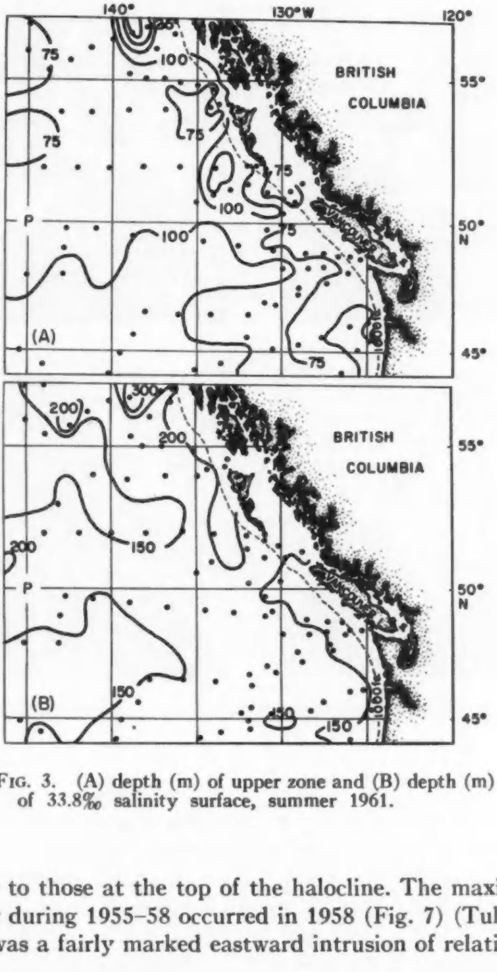


FIG. 3. (A) depth (m) of upper zone and (B) depth (m) of 33.8‰ salinity surface, summer 1961.

patterns similar to those at the top of the halocline. The maximum extent of the warm water during 1955–58 occurred in 1958 (Fig. 7) (Tully et al., 1960). In 1958, there was a fairly marked eastward intrusion of relatively cold water along lat 47°N.

In 1959 and 1960, the warm water along the coast had retreated slightly (Fig. 8). Further development of a warmwater intrusion started again in 1961 and continued through 1962. The most significant difference between these distributions and that for 1958, was the absence of the intrusion of relatively cold water along lat 47°N during the later years.

There are no serial oceanographic data after 1962. However, during 1965 and 1966, extensive bathythermograph data were taken. The distributions of temperature at 175 m (approximate depth of 33.8‰ isohaline) are shown in Fig. 9. The areas of warm water were less in 1965 and 1966 than for the years 1958–62 (no comparable data are available for 1963 and 1964).

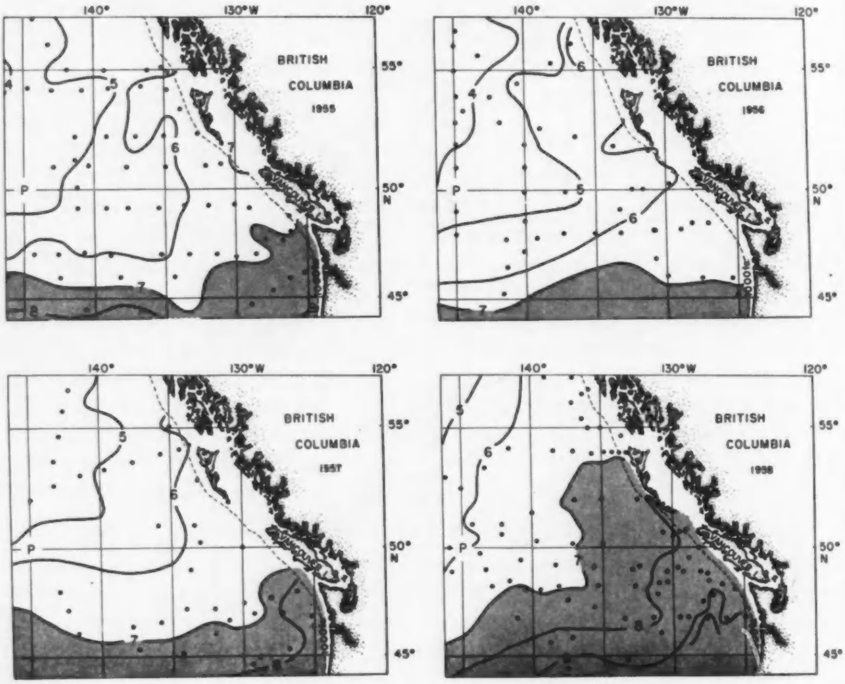


FIG. 4. Temperature distributions at top of halocline, 1955–58.

6. DISCUSSION

There are three major year-to-year changes that take place in all these temperature distributions. In the southwestern part of the region, there is a meridional shift in the isotherms. This may be accompanied by meridional and zonal shifts along the coast (Fig. 10). There may be an eastward intrusion of relatively cold water as occurred in 1958 (Fig. 7). A classification of these years into cold, intermediate, and warm, taking into account these changes, was made by computing the areas of warm water, greater than 7 C for the seasonal zone and greater than 6.5 C for the non-seasonal zone. Comparison of absolute values between the seasonal and non-seasonal waters (Fig. 11) should not be made.

The upper-zone waters (Fig. 11B) appear to have had their greatest extent in 1963, somewhat greater than in 1958. Their least extent was in 1956. It is felt that 1958 was slightly warmer than 1963, as inferred from data at Ocean Station P and coastal stations. The discrepancy here is probably due to the fact that sea surface temperature data from transitting ships do not give temperature distributions as accurately as those obtained from survey data. In 1965, these waters nearly retreated to the position observed in 1956.

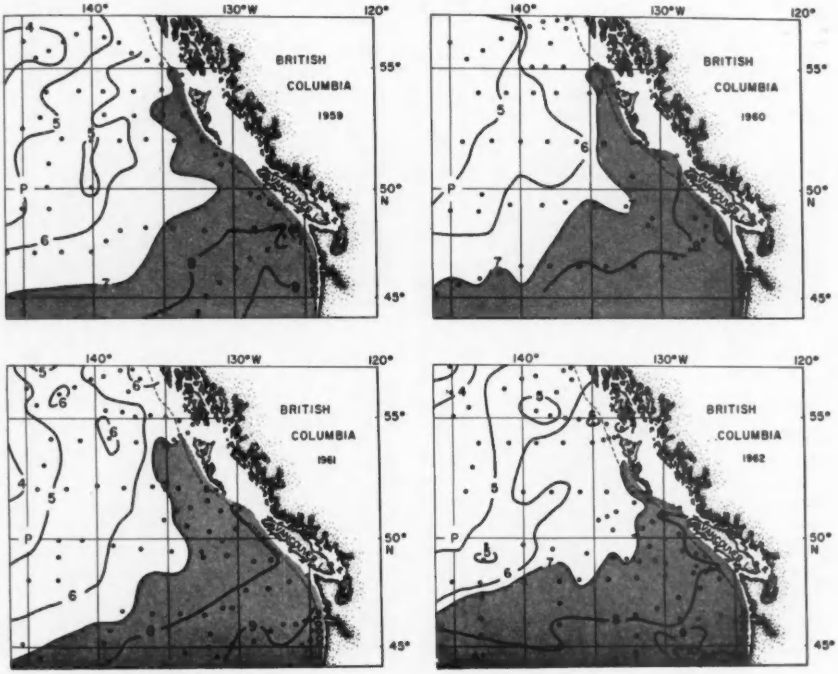


FIG. 5. Temperature distributions at top of halocline, 1959–62.

The minimum monthly mean sea-surface temperatures at Ocean Station P for these years are included in Fig. 11. They are indicative of the year-to-year trends in the extent of warm water in the upper zone.

In the lower zone (Fig. 11A) the year-to-year trends were similar to those observed at the top of the halocline, for a majority of the years. The overall extent of warm water was less in 1958 than in 1961 and 1962 owing to the eastward intrusion of relatively cold water in 1958, as noted in Fig. 7. Otherwise, the distributions of lower-zone warm water were similar for these years. It is reasonable to assume that warm water was also extensive in 1963 and somewhat less in 1964. The lower-zone waters did not retreat to the position observed in 1956 or anywhere near there.

The upper- and lower-zone waters have an additional significance in that they determine conditions in the bottom waters of the continental shelf. Conditions here are contingent upon convergent, divergent, or relaxation situations associated with the Ekman wind stress. They have been reported by Lane (1963) and Fofonoff and Tabata (1966) and are shown schematically in Fig. 12.

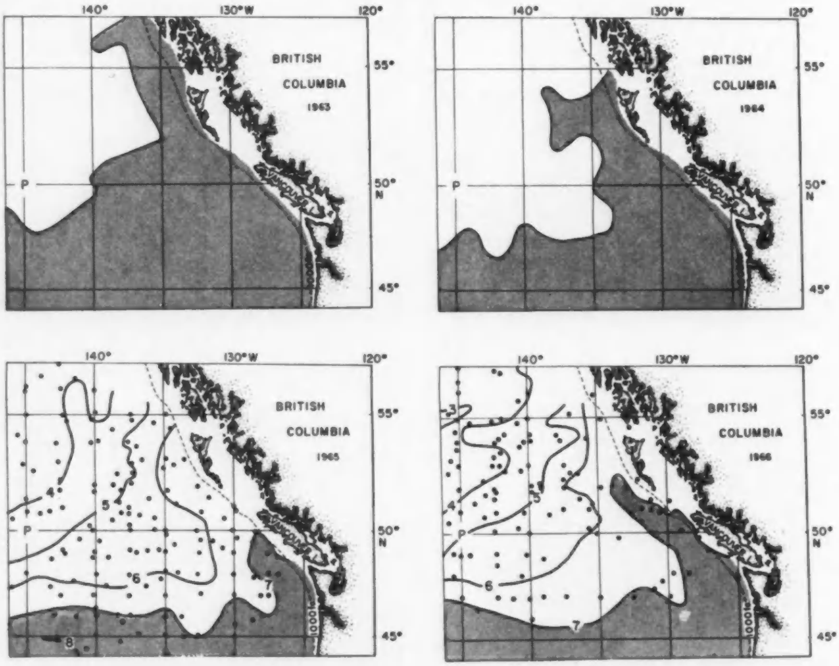


FIG. 6. *Upper*, distribution of the 7 C isotherm, March 1963 and 1964 (adapted from charts issued by the Bureau of Commercial Fisheries, La Jolla); *lower*, minimum winter temperature distributions, 1965 and 1966.

During winter, the convergent situation predominates, resulting in an onshore movement of oceanic, upper-zone waters over the continental shelf. During summer, the divergent situation prevails, and the oceanic halocline waters and lower-zone waters generally predominate. Under persistent winds, upwelling will occur. The relaxation situation is intermediate. Thus, there is a seasonal cycle in the bottom waters of the continental shelf, and in annual changes associated with the variability of the upper- and lower-zone oceanic waters.

The only continuous near-bottom temperature data available over the continental shelf are those obtained from bathythermograph lowerings at Swiftsure Bank (Fig. 10). Because of the bank's position, the bottom waters will only be partly dependent upon these situations. However, the data are useful to identify anomalous situations.

The minimum monthly mean bottom temperatures in winter (March) and the monthly mean bottom temperatures in summer (July and August) at Swiftsure Bank for the years 1955 through 1961 are included with the plots of areas of warm water at the top of the halocline and at 33.8‰, respectively

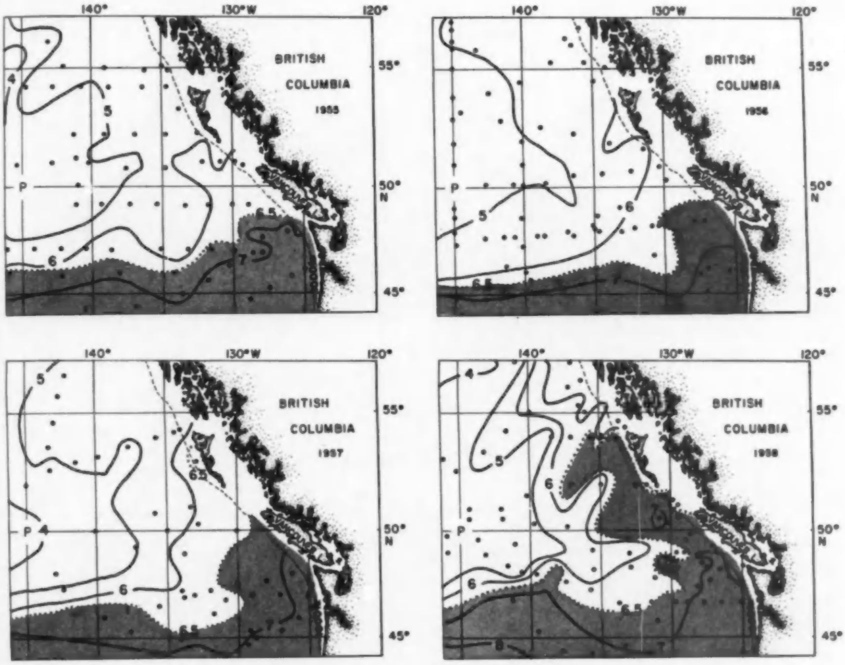


FIG. 7. Temperature distributions on the 33.8‰ salinity surface, 1955–58.

(Fig. 13). The annual trends in the bottom waters generally follow the changes in the oceanic waters, if it can be assumed that the seasonal divergent–convergent situations exist. Bottom temperatures during the summer of 1957 and winter of 1961 appear anomalous, and, in part, may be due to anomalies in the wind conditions. However, continuous data from the oceanic-coastal area are required before these situations can be adequately defined.

COASTAL AND INLET WATERS OF BRITISH COLUMBIA

In describing the changes with time of the characteristics of the waters of British Columbia, it is convenient to divide the area into three oceanographic regions (Fig. 14): (*a*) the outer coast, off the western coastline of the Queen Charlotte and Vancouver Islands; (*b*) the inner coast, between these islands and the mainland; and (*c*) the fjord-type inlets of the islands and the mainland.

The characteristics of these waters and of their temporal changes have been described for the outer and inner coasts by Pickard and McLeod (1953), for the inner coast by Waldichuk (1957), Tully and Dodimead (1957), and Elliott (1965), and for the inlets by Pickard (1961, 1963), Gilmartin (1962),

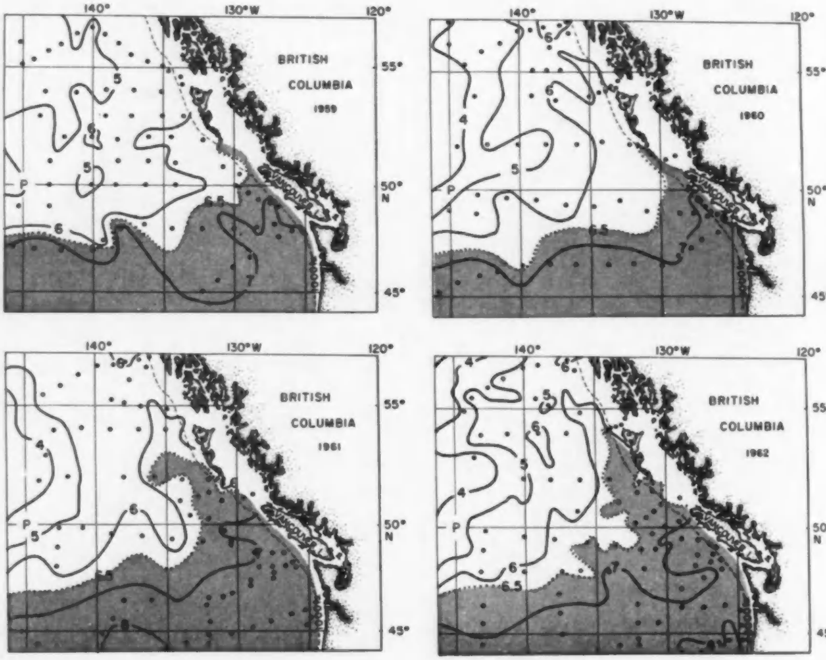


FIG. 8. Temperature distributions on the 33.8‰ salinity surface, 1959–62.

Herlinveaux (1962), and Lazier (1963). A comprehensive review of surface temperatures and salinities for shore stations of the outer and inner coast of British Columbia and Alaska, together with bibliography and abstracts of papers, has been presented by Hollister (MS, 1964).

In each region the water structure is estuarine and similar to that in the oceanic region to the west although the features of an upper zone, a halocline/thermocline zone, and a lower zone are more marked. The upper zone generally shows significant seasonal variations of water properties of larger magnitude than in the oceanic area but it is shallower, typically 5–30 m in depth. The lower zone, below 50 to 100 m, shows small seasonal variations in the two coastal regions. Some of the inlets show seasonal variations in the deep water; others do not. The intervening halocline/thermocline zone has steeper gradients of salinity and temperature than in the ocean.

1. UPPER ZONE

Temperature in all the regions shows an annual cycle with a maximum in August and a minimum in January/February. The differences between

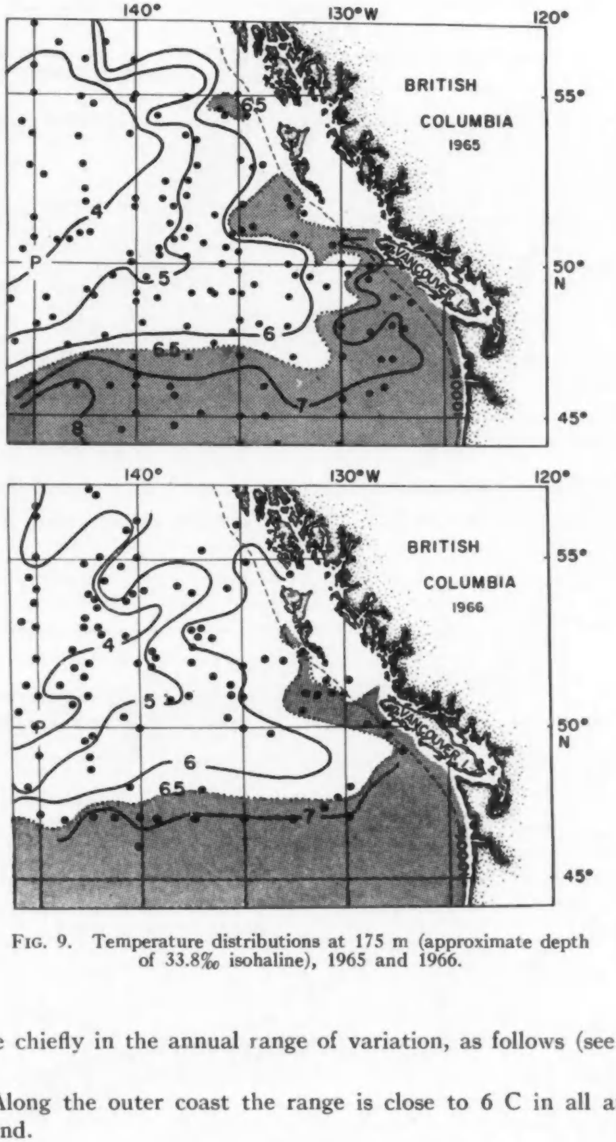

140°
130°W
120°
BRITISH
COLUMBIA
1965
55°
50°
N
45°
P
4
5
6
6.5
7
8
65
VANCOUVER I.
1000
140°
130°W
120°
BRITISH
COLUMBIA
1966
55°
50°
N
45°
P
4
5
6
6.5
7
VANCOUVER I.
1000

FIG. 9. Temperature distributions at 175 m (approximate depth of 33.8‰ isohaline), 1965 and 1966.

regions are chiefly in the annual range of variation, as follows (see also Fig. 15A):

(*a*) Along the outer coast the range is close to 6 C in all areas, e.g., Kains Island.

(*b*) In the inner coast region the annual range is larger, at 7–12 C, e.g., Entrance Island, except where strong tidal mixing reduces the range, e.g., Race Rocks.

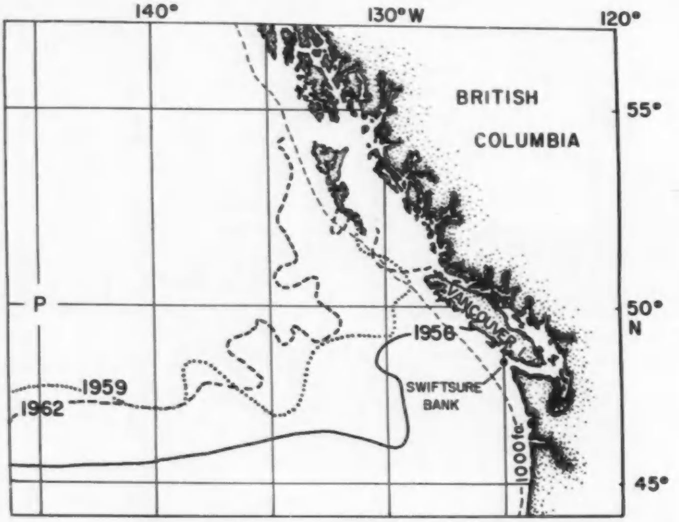

140°
130°W
120°
BRITISH
COLUMBIA
55°
50°
N
45°
P
1956
1959
1962
VANCOUVER I.
SWIFTSURE
BANK
1000 fa

FIG. 10. Distribution of 6.5 C isotherm at 33.8‰ salinity surface, 1956, 1959, and 1962.

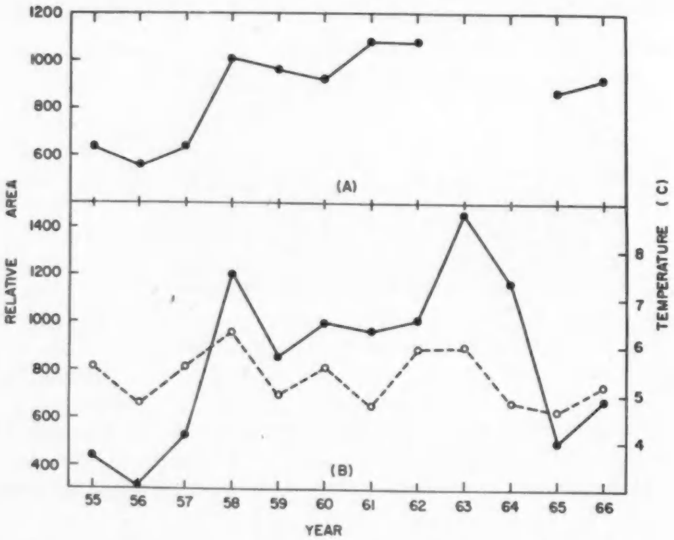


FIG. 11. (A) relative areas of warm water (>6.5 C) at salinity = 33.8‰ (1965 and 1966 based on B.T. temperatures at 175 m); (B) relative areas of warm water (>7.0 C) at top of halocline (solid circles), and minimum monthly mean sea-surface temperatures at Ocean Station P (open circles).

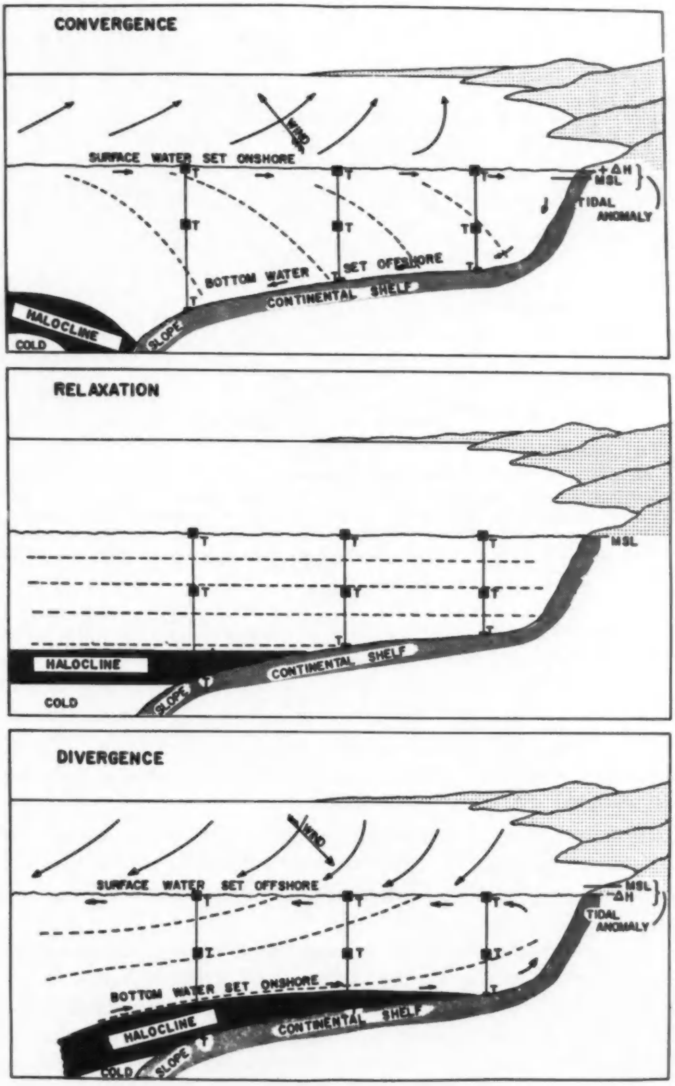

CONVERGENCE
WIND
SURFACE WATER SET ONSHORE
T
+ΔH
MSL
TIDAL ANOMALY
BOTTOM WATER SET OFFSHORE
CONTINENTAL SHELF
HALOCLINE
COLD
SLOPE
RELAXATION
T
MSL
HALOCLINE
CONTINENTAL SHELF
SLOPE
COLD
DIVERGENCE
WIND
SURFACE WATER SET OFFSHORE
T
MSL
-ΔH
TIDAL ANOMALY
BOTTOM WATER SET ONSHORE
HALOCLINE
CONTINENTAL SHELF
SLOPE
COLD

FIG. 12. Schematic of convergence, relaxation, and divergence situations off the west coast of Vancouver Island.

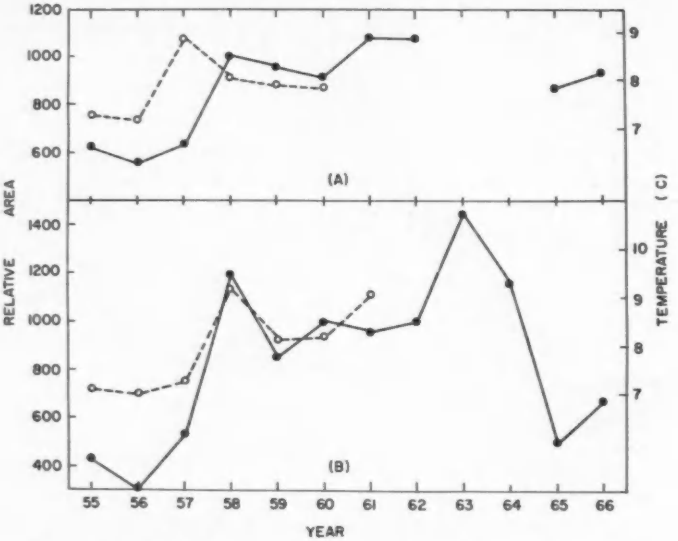


FIG. 13. (A) relative areas of warm water (>6.5 C) at salinity = 33.8‰ (solid circles), and monthly mean bottom temperatures in summer (July and August) at Swiftsure Bank (open circles); (B) relative areas of warm water (>7.0 C) at top of halocline (solid circles), and minimum monthly bottom mean temperatures in winter (March) at Swiftsure Bank (open circles).

(*c*) In the inlets the range may be from 6 to 15 C, e.g., Bute Inlet. The smaller ranges in the inlets occur where there is considerable river runoff of cold glacial water whereas the larger ranges occur where there is little river runoff.

Salinity cycles, however, are not the same in all regions as they are determined directly by river runoff, which has different seasonal cycles in different regions, and indirectly by precipitation:

(*a*) Along the outer coast in most places there is an August maximum of salinity owing to seasonal decrease in precipitation and consequent local river runoff, e.g., Kains Island (Fig. 15B). The mean annual range of salinity is from 0.3 to 3‰.

(*b*) In the inner coast region, in most areas there is a summer minimum of salinity in June/July due to the river runoff, with decreases of up to 6‰ from the winter values (e.g., Entrance Island, Fig. 15B). This runoff has a maximum in May–July from snow and ice melt in the interior snowfields and glaciers. In exposed areas where there is much tidal mixing the seasonal variation may be almost completely suppressed, as at Race Rocks (Fig. 15B).

(*c*) In the inlets there are two types of annual salinity cycle (Fig. 15C). In most cases there is a conspicuous minimum in June/August (e.g., Bute Inlet) with values falling to 0‰ at the inland end near the rivers, so that there

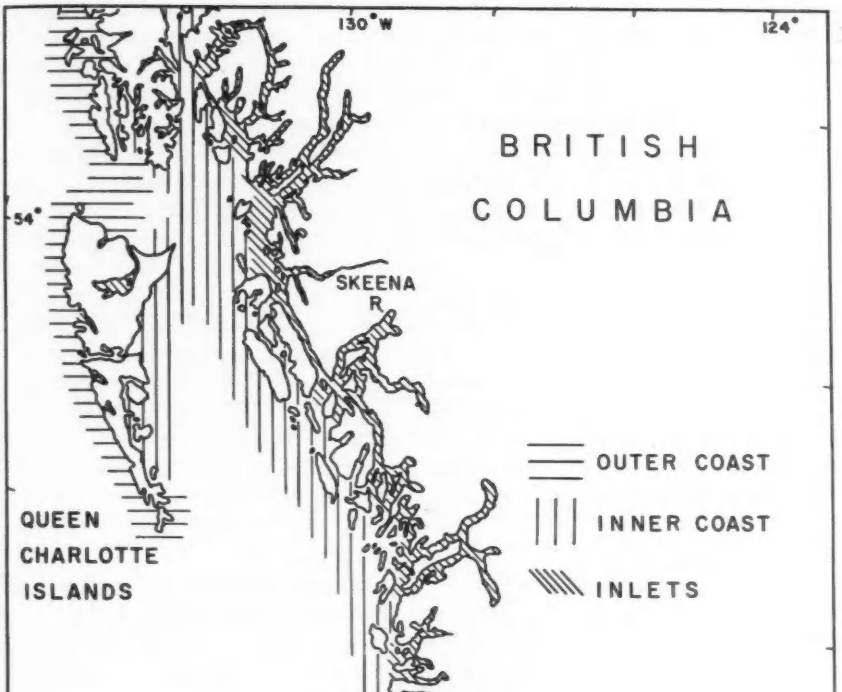

130°W
124°
BRITISH COLUMBIA
54°
SKEENA R.
OUTER COAST
INNER COAST
INLETS
QUEEN CHARLOTTE ISLANDS
50°N
BUTE INLET
KAINS IS.
STRAIT of GEORGIA
50°
VANCOUVER ISLAND
INDIAN ARM
FRASER R.
ENTRANCE IS.
RACE ROCKS
PACIFIC OCEAN
130°
124°

FIG. 14. Oceanographic regions of the coastal and inshore waters of British Columbia.

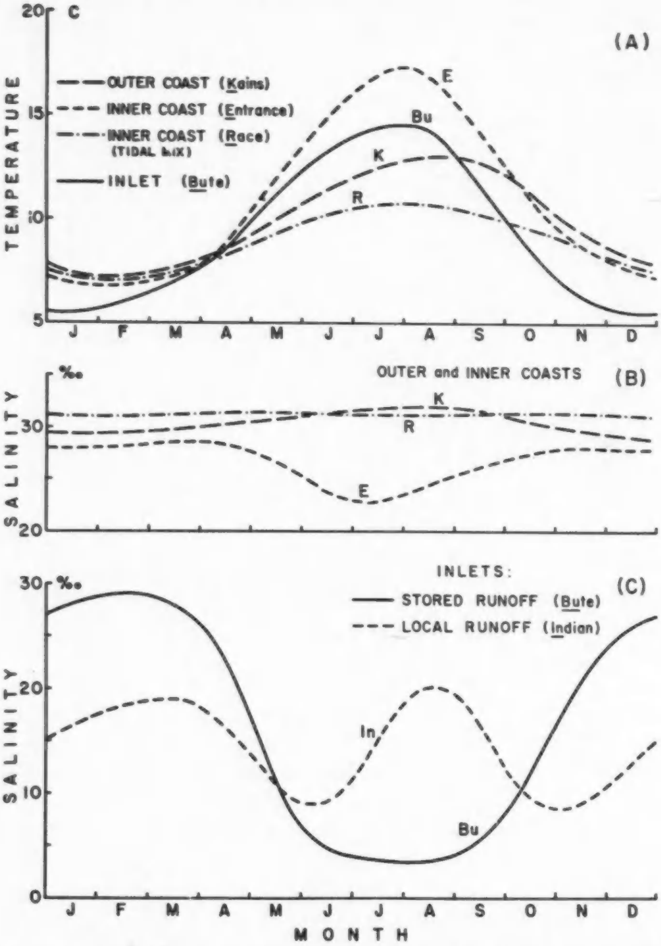


FIG. 15. Typical annual cycles of temperature and salinity at the surface in coastal and inshore waters of British Columbia.

may be a seasonal salinity change of as much as 25‰. This minimum is due to the large spring and summer river runoff from snowmelt on the mountains of the interior (stored runoff). Some of the smaller inlets show two minima in salinity (e.g., Indian Arm), because their river runoff is directly from precipitation on the local water shed (local runoff) and there are two maxima, one in April/May from snowmelt and the other in October/November from rain.

The oxygen content of the waters generally shows considerable variation from place to place and with time, and it is more difficult to generalize its seasonal variations than for the other water properties. In the surface water there may be two maxima, in spring and autumn, associated with plankton blooms, but below 2–4 m depth it is difficult to separate these, and a slight summer maximum is the best description.

A feature of the inner coastal and inlet waters is a seasonal variation in turbidity, also associated with river runoff. In many of the inlets, particularly those receiving river runoff from glaciers, the secchi disc depth in the upper layers of water decreases to a fraction of a meter during the large river runoff period (Pickard and Giovando, 1960). During lesser river runoff periods the secchi disc depth may increase to 1–2 m but still remains less than that in the inner coastal waters. The glacial silt which causes the very low secchi disc readings tends to precipitate out of the surface water as this flows to seaward, and secchi disc depths of several meters are usual toward the mouths of the inlets, with a small seasonal decrease often as a result of the phytoplankton blooms in spring and autumn. In the inner coastal region, the Fraser River discharges directly into the Strait of Georgia and gives rise to very low secchi disc readings within several miles of the river mouth, with some effect extending to tens of miles from the river mouth. The same occurs off the Skeena River.

2. HALOCLINE/THERMOCLINE ZONE

The water density, and hence the stratification, is determined almost entirely by salinity in the upper and in the halocline/thermocline zones, and to a large extent in the deep zone. Typical vertical profiles of salinity are shown schematically in Fig. 16. In the summer, the temperature profiles are approximately mirror images of the salinity profiles, whereas in the winter the water column tends to become isothermal (but not isohaline).

(*a*) In the outer coastal region the salinity profiles are generally of type 1C form, sometimes of type 2. In regions of strong tidal mixing inshore the water may become virtually isohaline, type 3.

(*b*) In the inner coast, profiles of type 1C are general. Type 3 occurs where there is strong tidal mixing, and type 1B or even 1A in the regions close to the mouths of the Fraser and Skeena rivers.

(*c*) In the inlets with large river inflow, profiles of type 1A are found in early summer toward the heads of the inlets where the large rivers enter. The halocline has a sharp upper boundary and salinity gradients as high as 30‰ per metre occur. Along the inlets, upward transfer of saline water by vertical mixing reduces the halocline gradient through type 1B to type 1C near the inlet mouths. In winter the extreme type 1A profiles are less common, because of decreased river runoff and of increased wind mixing between the upper zone and the halocline zone.

The type 2 profile is characteristic of inlets with small or negligible runoff. There are few of these inlets on the mainland coast, and more in the large islands and on the west coast of Vancouver Island.

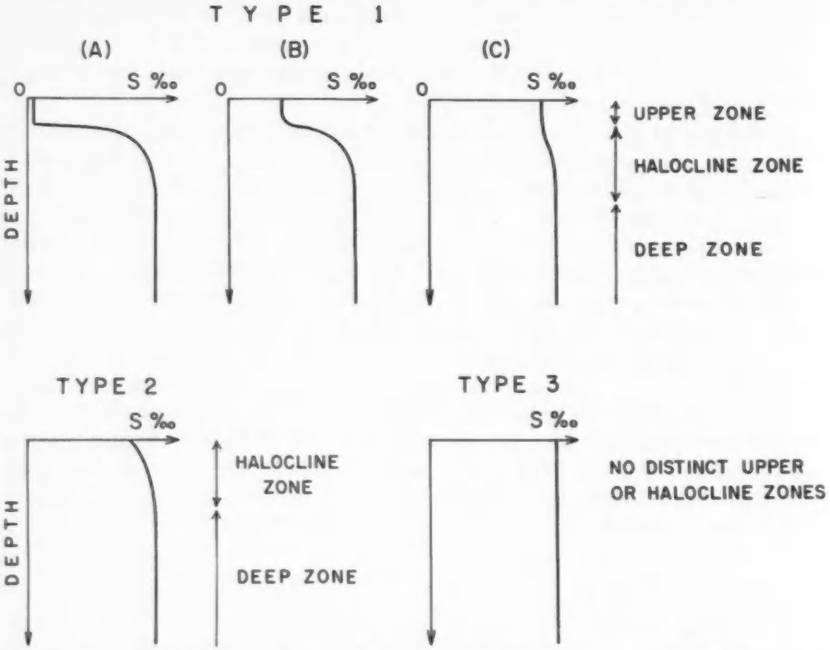


FIG. 16. Typical vertical profiles of salinity in coastal and inshore waters of British Columbia shown schematically.

3. LOWER ZONE

In the deeper water (beyond about 100 m), the variations are characteristic of the regions:

(*a*) On the outer coast, the mechanisms have already been described in terms of convergent–divergent conditions. In consequence, in summer there is an increase in salinity, a small decrease in temperature, and possibly a decrease in oxygen content from the subsurface oxygen minimum.

(*b*) In the inner coast region, the most extensive deep areas are to the south in the Strait of Georgia, where there is some summer inflow of deep water. This inflow is attributed chiefly to increased two-layer estuarine circulation during the summer, when the increased surface outflow from river runoff entrains and removes subsurface saline water and a strengthened deep-water inflow results.

(*c*) In the inlets of the west coast of Vancouver Island, although continuous time series records are not available, there is evidence of an annual inflow to the deep zones in the late summer. This results from the previously mentioned summer onshore movement of high salinity water. The increase in density of the water outside and above sill depth results in sub-surface inflow to the inlets. In some cases, this causes only a partial replacement of

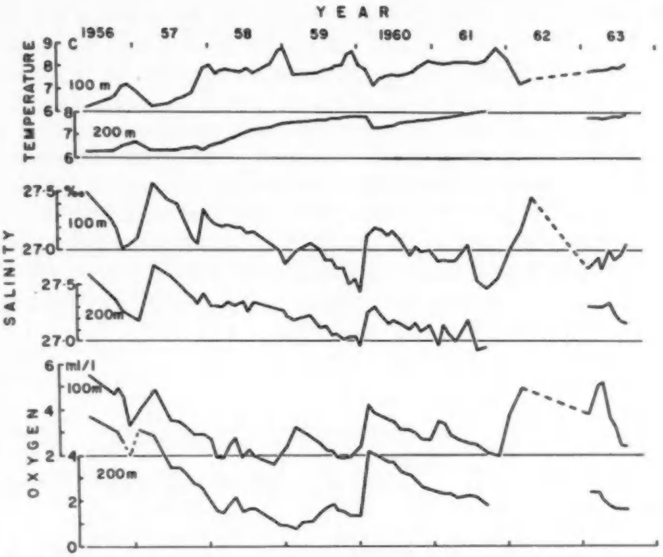


FIG. 17. Long term variations of temperature, salinity, and dissolved oxygen in the sub-halocline waters of a small mainland inlet (Indian Arm) with small river runoff.

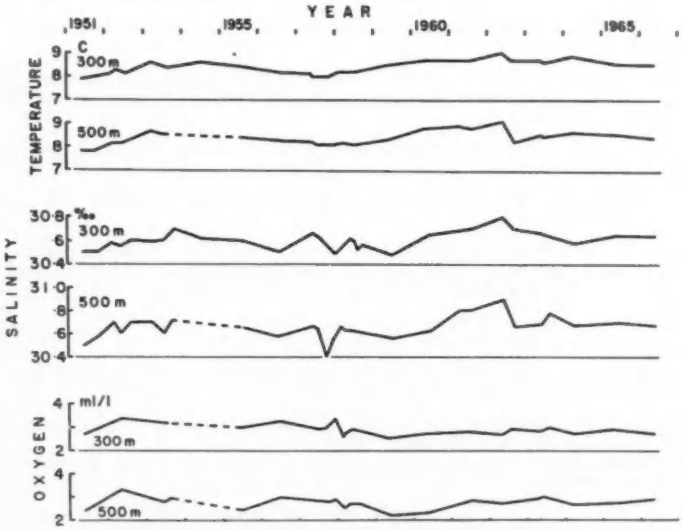


FIG. 18. Long term variations of temperature, salinity, and dissolved oxygen in the deep waters of a large mainland inlet (Bute Inlet) with large river runoff.

the deep water, but in a few inlets it results in almost complete exchange. In such cases, the inflowing water has an oxygen content of 4–5 ml/liter, but this is often decreased to zero by the next summer, i.e. in less than 12 months.

Finally, in the inlets of the mainland coast there is no annual cycle of change of deepwater properties. Exchange of water with the inner coastal region takes place at irregular intervals. One example of this is shown for a small inlet, Indian Arm (Fig. 17), where the exchange interval is of the order of 2–4 years. In other inlets the period appears to be longer than this, for instance in Bute Inlet (Fig. 18), although there are not sufficiently complete or extensive records to be sure. Examples of such probable large-scale exchange of deep water were evident in 1957 and 1962.

REFERENCES

DODIMEAD, A. J. MS, 1958. Report on oceanographic investigations in the northeast Pacific Ocean during August 1956, February 1957, and August 1957. Fish. Res. Bd. Canada, MS Rept. Ser. (Oceanog. Limnol.). No. 20. 10 p.

1961. Some features of the upper zone of the sub-Arctic Pacific Ocean. Intern. North Pacific Fish. Comm., Bull. No. 3. p. 11–24.

DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO. 1963. Review of oceanography of the Subarctic Pacific Region. Ibid., Bull. No. 13. 195 p.

DOE, L. A. E. 1955. Offshore waters of the Canadian Pacific Coast. J. Fish. Res. Bd. Canada, **12**(1): 1–34.

ELLIOTT, J. A. 1965. A study of the heat budget components for the British Columbia and southeast Alaska Coast. M.Sc. Thesis. University of British Columbia, Vancouver, B.C.

FLEMING, R. H. 1958. Notes concerning the halocline in the northeastern Pacific Ocean. J. Marine Res., **17**: 158–173.

FOFONOFF, N. P., AND S. TABATA. 1966. Variability of oceanographic conditions between Ocean Station P and Swiftsure Bank off the Pacific Coast of Canada. J. Fish. Res. Bd. Canada, **23**(6): 825–868.

GILMARTIN, M. 1962. Annual cyclic changes in the physical oceanography of a British Columbia fjord. Ibid., **19**(5): 921–974.

HERLINVEAUX, R. H. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. Ibid., **19**(1): 1–37.

HOLLISTER, H. J. MS, 1964. Classification of monthly mean sea surface temperatures and salinities at shore stations along the British Columbia and adjacent American coast, 1915–1962. Fish. Res. Bd. Canada, MS Rept. Ser. (Oceanog. Limnol.). No. 177. 123 p.

LANE, R. K. 1963. A model of seawater structure near the west coast of Vancouver Island, British Columbia. J. Fish. Res. Bd. Canada, **20**(4): 939–967.

LAZIER, J. R. N. 1963. Some aspects of the oceanographic structure of the Jervis Inlet system. M.Sc. Thesis. University of British Columbia, Vancouver, B.C.

PICKARD, G. L. 1961. Oceanographic features of inlets of the British Columbia mainland coast. J. Fish. Res. Bd. Canada, **18**(6): 907–999.

1963. Oceanographic characteristics of inlets of Vancouver Island, British Columbia. Ibid., **20**(5): 1109–1144.

PICKARD, G. L., AND D. C. MCLEOD. 1953. Seasonal variation of temperature and salinity of surface waters of the British Columbia coast. Ibid., **10**(3): 125–145.

PICKARD, G. L., AND L. F. GIOVANDO. 1960. Some observations of turbidity in British Columbia inlets. Limnol. Oceanog., **5**(2): 162–170.

TABATA, S. MS, 1964. A study of the main physical factors governing the oceanographic conditions at Ocean Station "P" in the northeast Pacific Ocean. D.Sc. Thesis. University of Tokyo. 264 p.

TULLY, J. P., AND A. J. DODIMEAD. 1957. Properties of water in the Strait of Georgia, British Columbia, and influencing factors. J. Fish. Res. Bd. Canada, **14**(3): 241–319.

TULLY, J. P., AND F. G. BARBER. 1960. An estuarine analogy in the Subarctic Pacific Ocean. Ibid., **17**(1): 91–112.

TULLY, J. P., A. J. DODIMEAD, AND S. TABATA. 1960. An anomalous increase of temperature in the ocean off the Pacific Coast of Canada through 1957 and 1958. Ibid., **17**(1): 61–80.

TULLY, J. P., AND L. F. GIOVANDO. 1963. Seasonal temperature structure in the eastern Subarctic Pacific Ocean. Marine distributions. The Royal Society of Canada, Spec. Publ. No. 5. M. J. Dunbar [ed.], Univ. Toronto Press, Toronto, Ont. p. 10–36.

UDA, M. 1963. Oceanography of the Subarctic Pacific Ocean. J. Fish. Res. Bd. Canada, **20**(1): 119–179.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. Ibid., **14**(3): 321–486.

Hypoxanthine in Iced Freshwater Fish[1]

L. C. Dugal

Fisheries Research Board of Canada
Freshwater Institute, Winnipeg, Man.

ABSTRACT

The formation of hypoxanthine in ordinary muscle was followed in 36 individual yellow walleye (*Stizostedion vitreum*) and in 22 individual whitefish (*Coregonus clupeaformis*) stored in ice. At the time of death, the average hypoxanthine content was approximately the same for the two species (0.25 μmole/g); it increased gradually to 1.52 μmole/g in 22 days and to 2.54 μmole/g in 18 days in yellow walleye and in whitefish respectively. The average rate of formation in yellow walleye (0.06 μmole/g per day) was the same as in ordinary muscle of swordfish; the rate of formation in whitefish (0.13 μmole/g per day) was slightly higher than that of Atlantic salmon, but lower than that of haddock, petrale sole, and several other marine species. Large variation in rate of formation was noticed between individual yellow walleyes. The average hypoxanthine content of both yellow walleyes and whitefish taken as groups was found to be proportional to the number of days in storage. No difference in average rate of formation was noticed between whitefish fillets from opposite sides of the fish, nor between fresh and thawed fish. The hypoxanthine content appears to be suitable as an index of freshness for groups of fish, not of individual fish.

RÉSUMÉ

On a suivi la formation de l'hypoxanthine dans le muscle ordinaire de 36 individus chez le doré (*Stizostedion vitreum*) et 22 individus chez le corégone (*Coregonus clupeaformis*) entreposés dans la glace. Au décès, la concentration moyenne en hypoxanthine est approximativement la même (0.25 μmole/g) chez les deux espèces. Au cours de l'entreposage elle augmente graduellement pour atteindre 1.52 μmole/g en 22 jours et 2.54 μmole/g en 18 jours respectivement chez le doré et le corégone. Le taux moyen de formation chez le doré (0.06 μmole/g par jour) est le même que dans le muscle ordinaire de l'espadron; le taux moyen chez le corégone (0.13 μmole/g par jour) est légèrement supérieur à celui du saumon atlantique, mais inférieur à ceux de l'aiglefin, de la plie pétrale, et de plusieurs autres espèces marines. Le doré démontre une grande variation du taux entre individus. Le contenu moyen en hypoxanthine chez le doré et chez le corégone augmente proportionellement avec le nombre de jours en entreposage dans la glace. Le taux moyen de formation a été le même pour les filets des côtés opposés du poisson et le même aussi pour le poisson frais et le poisson dégelé. Pour ces deux espèces de poisson d'eau douce, le contenu en hypoxanthine semble être un bon indice de fraîcheur pour des groupes de poisson, non pour les individus.

INTRODUCTION

OBJECTIVE TESTS for determining the state of freshness of freshwater fish have been investigated in different parts of the world (Paladino, 1945; Bose and Dutt, 1954; Wierzchowski, 1956; Moorjani et al., 1958; Somaatmadja et al., 1961; Deufel, 1963; Moriyama, 1964a, b, c, d). The tests, based on

---

[1] Received for publication April 24, 1967.

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

determination of volatile nitrogen bases, ammonia, volatile reducing substances, or volatile fatty acids, suffer from the fact that the compounds involved appear late in the course of storage, and thus are of little use in the early stage of storage for predicting the remaining shelf-life of a product (Gould, 1965).

The well-known trimethylamine test, used with success in connection with several marine species (Castell et al., 1958) is of no value with freshwater fish because these do not contain, or contain very little, trimethylamine oxide, the precursor of trimethylamine (Lintzel et al., 1939; Somaatmadja et al., 1961).

As a result of investigations by Torry research workers (Jones and Murray, 1961, 1962, 1964) on the degradation of nucleotides in marine fish, the use of the hypoxanthine level as an index of quality was advocated for some species (Jones, 1965). Spinelli et al. (1964) followed the formation of hypoxanthine in petrale sole and Pacific ocean perch and reached the conclusion that the test appeared to be suitable for these two species.

The purpose of the present investigation was to determine the rate of hypoxanthine formation in the muscle of freshwater fish in the course of storage in ice and to assess the value of the hypoxanthine test as an index of state of freshness. The formation of hypoxanthine was followed in individual fish, using a sufficient number of these to obtain data of statistical significance. Two species were investigated: yellow walleye (*Stizostedion vitreum*) and whitefish (*Coregonus clupeaformis*).

MATERIALS AND METHODS

Thirty-six yellow walleye weighing between 750 and 1500 g were obtained live from a trap-net fishery on Lake St. Clair, Ont., in late April 1966. These fish were all post-spawned. Twenty-four of these fish (group A) were killed with a blow on the head as soon as they came out of the water and a muscle sample was removed immediately and frozen in liquid nitrogen. Twelve other fish (group B), captured at the same time, were held in captivity for 2 weeks without feeding at the laboratory in London, Ont. They were killed with a blow on the head and a sample removed immediately and frozen in liquid nitrogen.

The fish in group A were kept in ice in the round for 2 days before eviscerating and cleaning. The fish in group B were cleaned immediately after killing. All fish were well iced in fiberglass boxes and held in a cold room at 2 C. The melt water was allowed to run out and the ice was completely renewed at each sampling session at intervals of about 2 days.

Twenty-two post-spawned whitefish weighing between 1000 and 2000 g were obtained in December 1965 from a commercial gill-net fishery on Lake Superior, Ont. These fish were all alive as they came out of the nets. They were eviscerated within hours of capture, packed in ice according to usual commercial practices, and shipped to the laboratory at London, Ont. On arrival the fish were filleted, and the fillets were packed in individual polyethylene bags for storage in ice. The formation of hypoxanthine in opposite sides of 11 fish was followed in groups C and D. Opposite sides of 11 more fish (groups E and F) were also compared, but the fillets from one side (group F) had first been held in frozen storage at –35 C for 5 weeks, then thawed overnight in a refrigerator and stored in ice like group E.

For groups A and B, samples of approximately 25 g were removed from the dorsal muscle of each fish moving back on successive sampling sessions from the area behind the neck to the tail portion on one side, and repeating the procedure on the other side. The samples on "day 0" were frozen in liquid nitrogen; all other samples were frozen in air at –35 C and stored at that temperature in polyethylene bags until analysed. The removal of a sample from the muscle exposed part of that muscle to the action of air and melt water; in order to attenuate the possible effect on hypoxanthine content, a slice of muscle about ¼-inch thick was removed from the exposed side of the muscle before removing a new sample. For groups C, D, E, F, the 25-g muscle samples were removed from the fillets without reference to position.

PREPARATION OF MUSCLE EXTRACTS

Hypoxanthine is known to accumulate at different rates in dark muscle as compared with ordinary muscle (Saito et al., 1959; Dyer et al., 1966); at extraction time all dark muscle was separated from the ordinary muscle, and only ordinary muscle was used for the determinations. Five grams of frozen white muscle were extracted with 40 ml of 0.6 N perchloric acid at 0 C in a Servall Omni-mixer. After centrifugation, the extract was brought to *p*H 6.5–7.0 with KOH (50% w/v), and allowed to stand 15 min at 0 C to insure precipitation of the perchlorate. After filtration, the solution was made up to 100 ml with distilled water.

HYPOXANTHINE DETERMINATION

Hypoxanthine was determined according to Kalckar's (1947) method as modified by Jones et al. (1964). Hypoxanthine is oxidized to uric acid by means of xanthine oxidase, and the absorption as a result of uric acid is determined at 290 mμ. Because 5 g instead of 25 g of muscle was used for extraction, 2.5 ml instead of 0.5 ml of the extract were used in the oxidizing test and no water was added. The xanthine oxidase was obtained from Worthington Biochemical Corporation, Freehold, N.J.

RESULTS AND DISCUSSION

In yellow walleye killed at the fishery and in those killed after holding in a tank for 2 weeks, the average hypoxanthine content went from 0.27 μmole/g at the time of death to 1.52 μmole/g after 22 days in ice at which time the fish as a group would have to be rejected. In whitefish the corresponding values were 0.23 μmole/g and 2.54 μmole/g after 18 days in ice. The daily group means, for both yellow walleye and whitefish, increased gradually with time in storage. Since the standard deviation (Snedecor, 1946) tended to increase proportionally to the daily group means, the results were transformed to their logarithmic equivalents (Snedecor, 1946) in order to make the ranges more similar and independent of the daily group means. Original regression lines obtained with the logarithmic values were not linear; however, they were linearized when the geometric means for day 0 was subtracted from all subsequent values before converting to logarithms.

Figure 1 shows the relationship for yellow walleye killed at the fishery (group A) and Fig. 2 shows the relationship for yellow walleye held in a tank for 2 weeks (group B) before killing. The slope in each is not significantly different from 1.0 indicating that the formation of hypoxanthine post-mortem is proportional to time in storage. In a log–log relationship, if the slope is

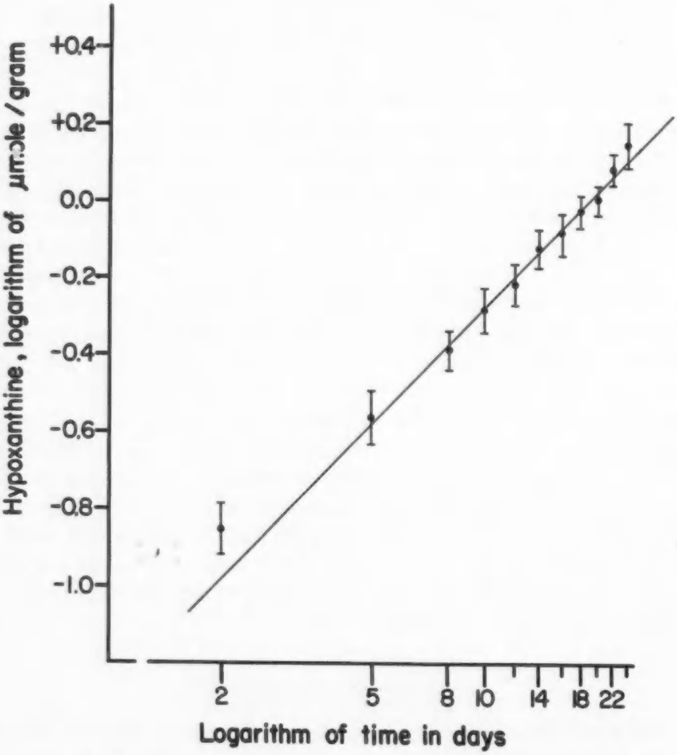


FIG. 1. Hypoxanthine formation in yellow walleye killed at the fishery (group A). Each point represents the average of 24 individuals, and the bars show the confidence limits at the 5% level. The initial average value for "day 0" (0.27 µmole/g) was subtracted from all subsequent results before converting to logarithms. The data for "day 2" was excluded for calculating the regression line.

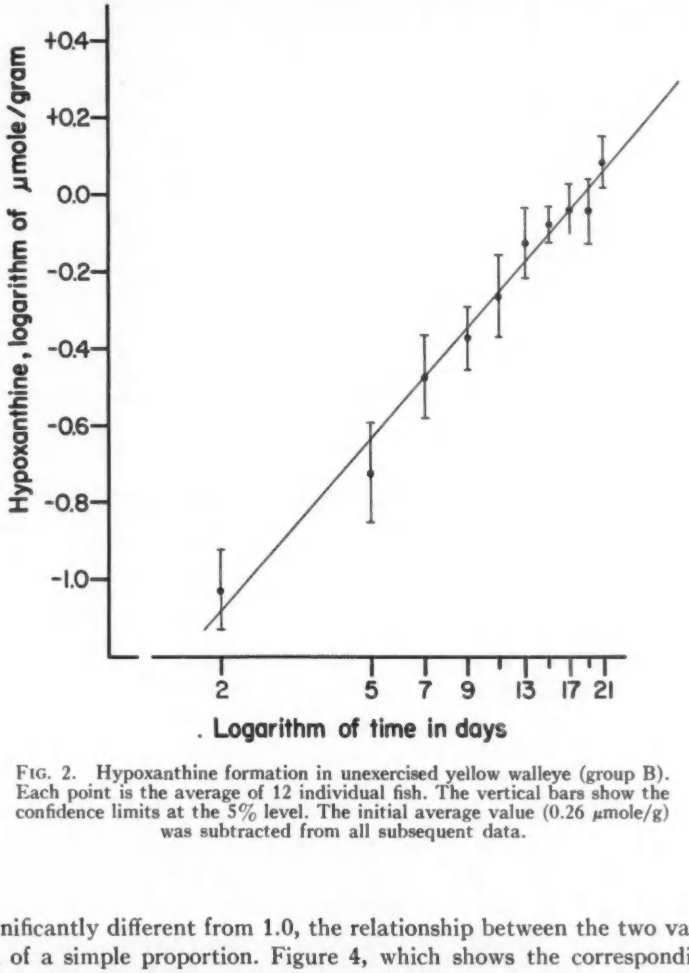


FIG. 2. Hypoxanthine formation in unexercised yellow walleye (group B). Each point is the average of 12 individual fish. The vertical bars show the confidence limits at the 5% level. The initial average value (0.26 µmole/g) was subtracted from all subsequent data.

not significantly different from 1.0, the relationship between the two variables is that of a simple proportion. Figure 4, which shows the corresponding relationship for whitefish, reveals that the formation of hypoxanthine is also proportional to time in storage. In the case of the whitefish, the initial value for day 0 to be subtracted from all other values before converting to logarithms had to be estimated by extrapolation from the daily arithmetic means because no sample had been removed until the 4th day in storage. The storage test with each species was discontinued when the fish as a group were definitely no longer fit for human consumption in the judgment of two experienced observers relying on smell and firmness of the flesh.

In Fig. 3 and 8, the solid curves represent individual fish showing the highest and the lowest rate of hypoxanthine formation and the dotted curve represents the group average. The values in these two figures are in terms of

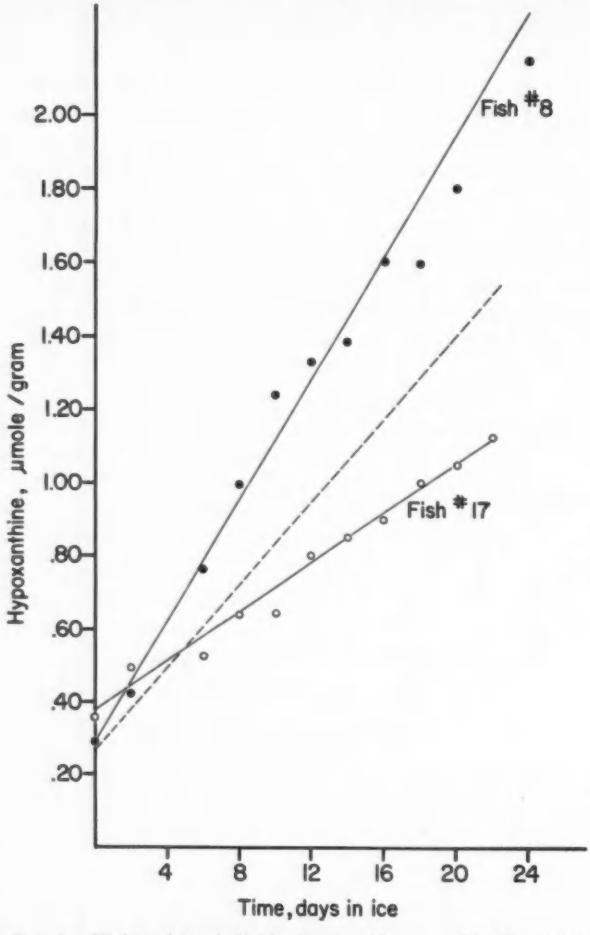


FIG. 3. High and low individual rates of hypoxanthine formation in yellow walleye (○—○ and ●—●), and average rate of formation in 36 individuals (-----).

μmoles/gram. In approximately 50% of all individuals, the change in hypoxanthine content was uniform from sampling day to sampling day, but in the other samples the change was irregular.

The daily range is not shown in Fig. 3 and 8; in yellow walleye the hypoxanthine content ranged from 0.15 to 0.44 μmole/g at day 0 and from 1.00 to 2.07 μmoles/g at 22 days; in whitefish the hypoxanthine content ranged from 0.58 to 0.94 μmole/g at day 0 and from 1.90 to 3.30 μmoles/g at 18 days.

Figures 4 and 5 show the log–log relationship between hypoxanthine content and time of storage in ice for fresh (groups C, D, and E together) and for thawed (group F) whitefish fillets.

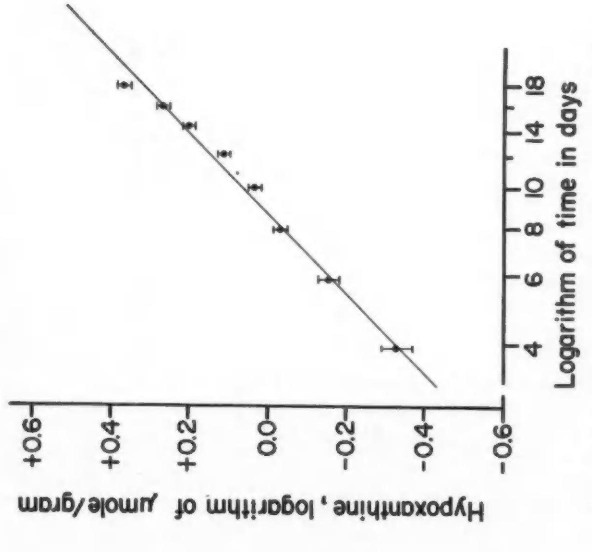


FIG. 4. Hypoxanthine formation in fresh whitefish, groups C, D, E together (C and D are opposite sides of 11 fish, E are fillets from 11 more fish). Each point is the average of 33 individual samples from 22 individual fish. The vertical bars show the confidence limits at the 5% level. The "day 0" average value (calculated as 0.23 μmole/g) was subtracted from all subsequent data.

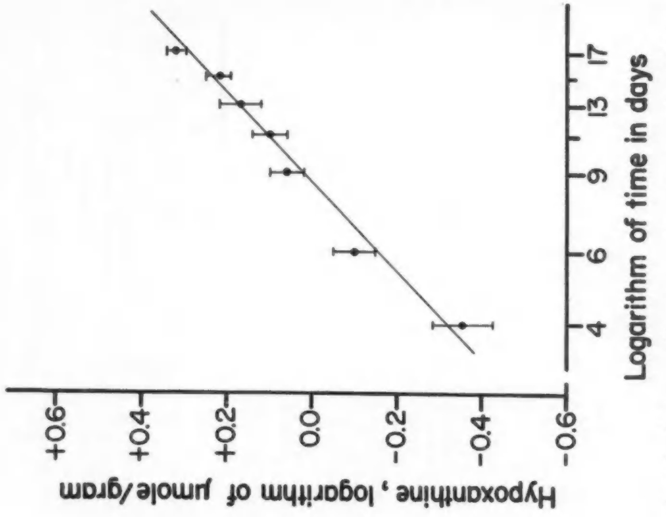


FIG. 5. Hypoxanthine formation in thawed whitefish (group F). Each point is the average of 11 individual fish. The vertical bars show the confidence limits at the 5% level. The "day 0" value (calculated as 0.34 μmole/g) was subtracted from all subsequent data.

Figures 6 and 7 show the log–log relationship between hypoxanthine content and time in storage for opposite sides of the same individual whitefish (groups C and D).

Statistical analysis of the adjusted group means, the slopes, and the variance showed that there was no difference in variance or slope between

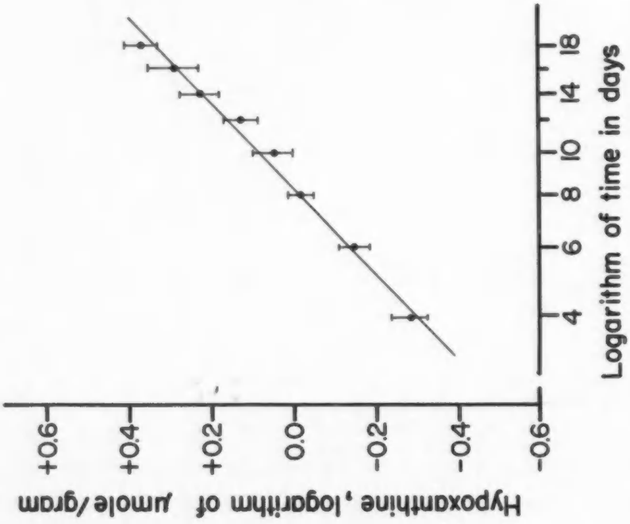


FIG. 6. Hypoxanthine formation in whitefish fillets from one side only (group C). Each point represents the average of 11 individual fish. The vertical bars show the confidence limits at the 5% level. The "day 0" average value (calculated as 0.23 µmole/g) was subtracted from all subsequent data.

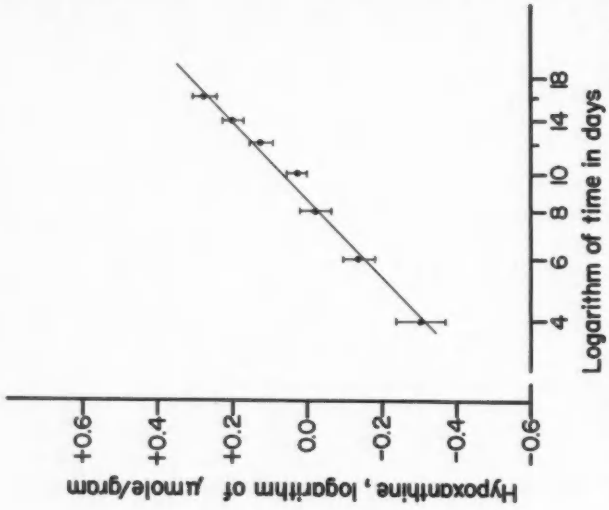


FIG. 7. Hypoxanthine formation in whitefish fillets from the opposite side of group C (group D). Each point represents the average of 11 individual fish. The vertical bars show the confidence limits at the 5% level. The "day 0" average value (calculated as 0.23 µmole/g) was subtracted from all subsequent data.

all samples of fresh whitefish together (groups C, D, and E) and thawed whitefish (group F). The initial level of the thawed fish after thawing was higher than that of the fresh fish; since no hypoxanthine is formed in frozen fish kept at –30 C (Jones and Murray, 1961; Spinelli et al., 1964), we must assume that some hypoxanthine was formed while the fish was being frozen and during thawing. Statistical analysis of the results also showed no significant

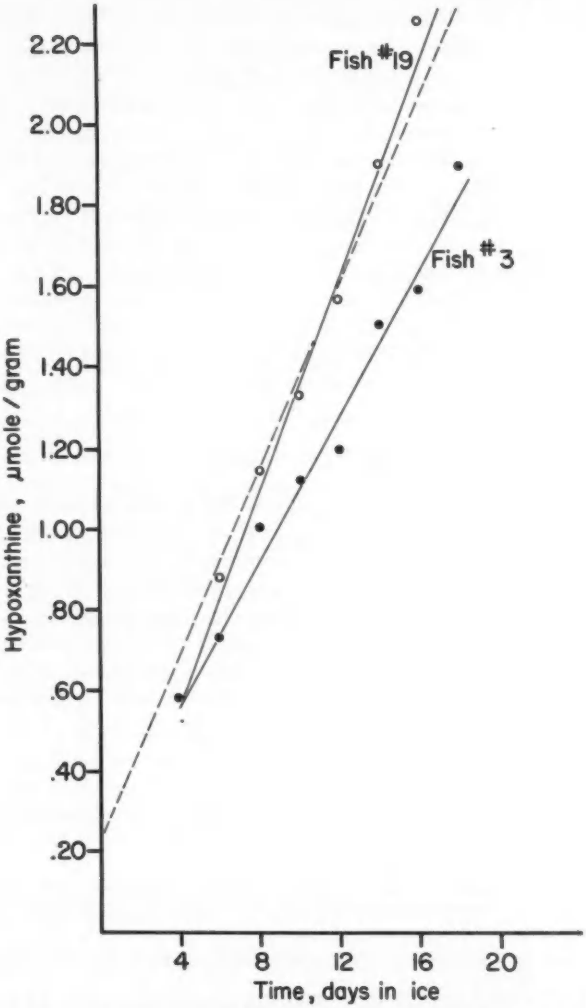


FIG. 8. High and low individual rates of hypoxanthine formation in whitefish (○—○ and ●—●), and average rate of 22 fresh whitefish (-----).

difference in variance, group means, or slopes between the two opposite sides of whitefish (groups C and D), and that for yellow walleye killed at the fishery (group A) and those killed after 2 weeks in a tank (group B), the only difference was in a slightly greater variance in group A than in group B.

The average rate of hypoxanthine formation in yellow walleye is very low (0.06 µmole/g per day) and appears to be equal to that (calculated) of ordinary muscle of swordfish (Dyer et al., 1966) and of Pacific salmon (Creelman and Tomlinson, 1960). The average rate in whitefish (0.13 μmole/g per day) is similar to that of Atlantic salmon (Murray et al., 1966), but lower than the rates for cod (Jones et al., 1964), ocean perch and petrale sole (Spinelli, 1964), haddock, lemon sole, and plaice (Kassemsarn et al., 1963).

The fact that hypoxanthine is formed at different rates in different individuals within a species would preclude using its level as an index of quality in individual fish. However, according to results obtained so far, there is a strong possibility that the average hypoxanthine of a group of fish would reflect the true state of freshness of that particular group. Since the rate of hypoxanthine formation varies from species to species, species rates would first have to be determined taking into account the possibility that the rates could be different in groups from different geographic areas, or of different physiological states at different times of the year.

ACKNOWLEDGMENTS

Special thanks to Mr F. Jubenville of Jubenville Fisheries, Jeannette's Creek, Ont. for sharing his facilities and time at the fishery; the Ontario Department of Lands and Forests for waving regulations on minimum size of yellow walleye; the Lake Superior Management group, Fisheries Research Board of Canada, Biological Station, London, Ont., for making the arrangements with a commercial fishery for securing whitefish; D. P. Scott, of the Fisheries Research Board of Canada, Freshwater Institute, Winnipeg, Man., for the statistical analysis of the results; D. M. Scott for most of the determinations.

REFERENCES

BOSE, A. N., AND J. M. A. DUTT. 1954. Objective methods for determination of state of spoilage of freshwater fish. J. Proc. Inst. Chemists India, No. 26: 27. *In* FAO World Fish. Abstr., Sept., Oct. 1955. p. 47.

CASTELL, C. H., M. F. GREENOUGH, S. S. RODGERS, AND A. S. MACFARLAND. 1958. Grading fish for quality. I. Trimethylamine values of fillets cut from graded fish. J. Fish. Res. Bd. Canada, **15**: 701–716.

CREELMAN, V., AND N. TOMLINSON. 1960. Inosine in the muscle of pacific salmon stored in ice. Ibid., **17**: 449–457.

DEUFEL, J. 1963. Comparative studies on the determination of the degree of freshness of fresh water fish. Z. Lebensm. Untersuch.-Forsch., **123**(5): 354–361. *In* Chem. Abstr., **60**: 8559b, 1964.

DYER, W. J., D. I. FRASER, AND D. P. LOHNES. 1966. Nucleotide degradation and quality in ordinary and red muscle of iced and frozen swordfish (*Xiphias gladius*). J. Fish. Res. Bd. Canada, **22**: 1821–1833.

GOULD, E. 1965. Testing the freshness of frozen fish. Fishing News (Books) Ltd., London. 51 p.

JONES, N. R. 1965. Hypoxanthine and other purine-containing fractions in fish muscle as indices of freshness. *In* R. Kreuzer [ed.] The technology of fish utilization. Fishing News (Books) Ltd., London. p. 179–183.

JONES, N. R., AND J. MURRAY. 1961. Nucleotide degradation in frozen cod muscle. Biochem. J., **80**: 26–27.

1962. Degradation of adenine and hypoxanthine nucleotides in the muscle of chill-stored trawled cod (*Gadus callarias*). J. Sci. Food Agr., **13**: 475–480.

1964. Rapid measure of nucleotide dephosphorylation in iced fish muscle. Their value as indices of freshness and of inosine 5′–monophosphate concentration. Ibid., **15**: 684–690.

JONES, N. R., J. MURRAY, AND (IN PART) MRS E. I. LIVINGSTON AND C. K. MURRAY. 1964. Rapid estimation of hypoxanthine concentration as indices of the freshness of chill-stored fish. Ibid., **15**: 763–774.

KALCKAR, H. M. 1947. Differential spectrophotometry of purine compounds by means of specific enzymes. I. Determination of hydroxy-purine compounds. J. Biol. Chem., **167**: 429–443.

KASSEMSARN, B., B. SANZ PEREZ, J. MURRAY, AND N. R. JONES. 1963. Nucleotide degradation in the muscle of iced haddock (*Gadus aeglefinus*), lemon sole (*Pleuronectes micro-cephalus*), and plaice (*Pleuronectes platessa*). J. Food Sci., **28**: 28–37.

LINTZEL, W., H. PFEIFFER, AND I. ZIPPEL. 1939. Untersuchungen über trimethylammonium basen. IV. Mitteilung: über das vorkommen von trimethylaminoxyd in der muskulatur von susswasserfisch. Biochem. Z., **301**: 29–36.

MOORJANI, M. N., J. R. IYENGAR, K. VISWESWARIAH, D. S. BHATIA, AND V. SUBRAHMANYAN. 1958. Changes in the total volatile base, volatile reducing substances and bacterial count as indices of freshwater fish spoilage. Food Technol., **12**: 385–387.

MORIYAMA, S. 1964a. Putrifaction tests of fish and their application to freshwater fishes. I. Determination of the volatile basic nitrogen. Nara Igaku Zasshi, **15**(1): 72–79. *In* FAO World Fish. Abstr, (1965), **16**(2): 47.

1964b. II. Determination of the volatile reducing substance. Ibid., **15**(1): 80–84. *In* FAO World Fish. Abstr. (1965), **16**(2): 47.

1964c. III. Determination of volatile fatty acids by gas chromatography. Ibid., **15**(1): 85–90. *In* FAO World Fish. Abstr. (1965), **16**(2): 47.

1964d. IV. Determination of histamine and other substances. Ibid., **15**(1): 91–96. *In* FAO World Fish. Abstr. (1965), **16**(2): 47.

MURRAY, J., N. R. JONES, AND J. R. BURT. 1966. Hypoxanthine in the muscle of chilled atlantic salmon (*Salmo salar*). J. Fish. Res. Bd. Canada, **23**: 1795–1797.

PALADINO, J. A. I. 1945. El estado de preservacion del pescado. Rev. Fac. Cien. Quim., Univ. Nacl. La Plata, **18**: 105–117. *In* G. Borgstrom [ed.] Fish as food. Vol. 1. Academic Press, Inc., New York, 1961. p. 623.

SAITO, T. K., K. ARAI, AND T. YAJIMA. 1959. Changes in purine nucleotides of red lateral muscle of rainbow trout. Nature, **184**: 1415.

SNEDECOR, G. W. 1946. Statistical methods. 4th ed. The Iowa State College Press, Ames, Iowa.

SOMAATMADJA, D., J. J. POWERS, AND D. C. PRATT. 1961. Chemical methods for the determination of the freshness of fish. J. Milk Food Technol., **24**(1): 2–6.

SPINELLI, J., M. EKLUND, AND D. MIYAUCHI. 1964. Measurement of hypoxanthine in fish as a method of assessing freshness. J. Food Sci., **29**: 710–714.

WIERZCHOWSKI, J. 1956. Chemical examination of freshness of fish. Przemysl Spozywczy, **10**(4): 162–165. *In* FAO World Fish. Abstr., May, June 1958. p. 47.

Bedrock and Sediments of Kouchibouguac Bay, New Brunswick[1,2]

BY KATE KRANCK

Department of Energy, Mines and Resources
Bedford Institute of Oceanography, Dartmouth, N.S.

ABSTRACT

On the basis of bottom samples and echograms from Kouchibouguac Bay and Northumberland Strait, the bottom topography, bottom lithology, and sediment distribution of the area are described and conclusions drawn regarding the composition of the underlying bedrock and the history of the sediments. A series of maps drawn after hydrographic charts dating back to 1839 show a buildup of the offshore barriers and underwater bars southeastward in the direction of long shore currents. Comparisons between maps illustrating bottom topography and bottom sediments show areas of topographic highs to be composed of bedrock and gravel whereas the topographic depressions consist chiefly of sand. Studies of the petrological composition of bedrock fragments and the gravel fraction reveal that green sandstone is the most common rock type in the samples from the inner part of Kouchibouguac Bay and probably underlies much of the area. On the basis of the abundant reddish-brown rocks in the samples from the outer part of the bay and the central area of Northumberland Strait it is concluded that the Scouduc Formation forms the bedrock in this area, whereas the red sandstone in samples near the coast of Prince Edward Island have been derived from the formations that form this island. Sediment colour and heavy mineral composition of the samples resemble that of the local sedimentary formations and indicate that the sand is derived from these rocks.

The gravel in the area consists of glacial material, more or less reworked by wave action. The sand in the bay also appears to be relict material. This is concluded from the occurrence of sand deposits interpreted on the basis of sedimentary parameters, relation to topography, and association with present-day river mouths, as former river deposits. In a 1–2 mile-wide zone along the offshore barrier, wave action controls the deposition and distribution as shown by both normal decrease of mean diameter seaward and negative skewness values in the sediments.

INTRODUCTION

THIS PAPER is a report of a sedimentological survey of the southern half of Kouchibouguac Bay, N.B. (Fig. 1). Its purpose was to provide information on the bottom lithology and sedimentary processes in the area, for use in a lobster research program. An area 9 × 2 km covering the southern part of Kouchibouguac Bay was studied in detail and 211 bottom samples were obtained from 220 stations (Fig. 2). To supplement the nearshore sampling, 45 stations were sampled along traverses across Northumberland Strait (Fig. 3). From the field and laboratory data, the bottom topography, and the sediment distributions and composition are outlined and discussed in relation to the historical development and agents of deposition.

---

[1] Received for publication March 7, 1967.

[2] Bedford Institute of Oceanography Contribution No. 90.

J. FISH. RES. BD. CANADA, **24**(11), 1967.
Printed in Canada.

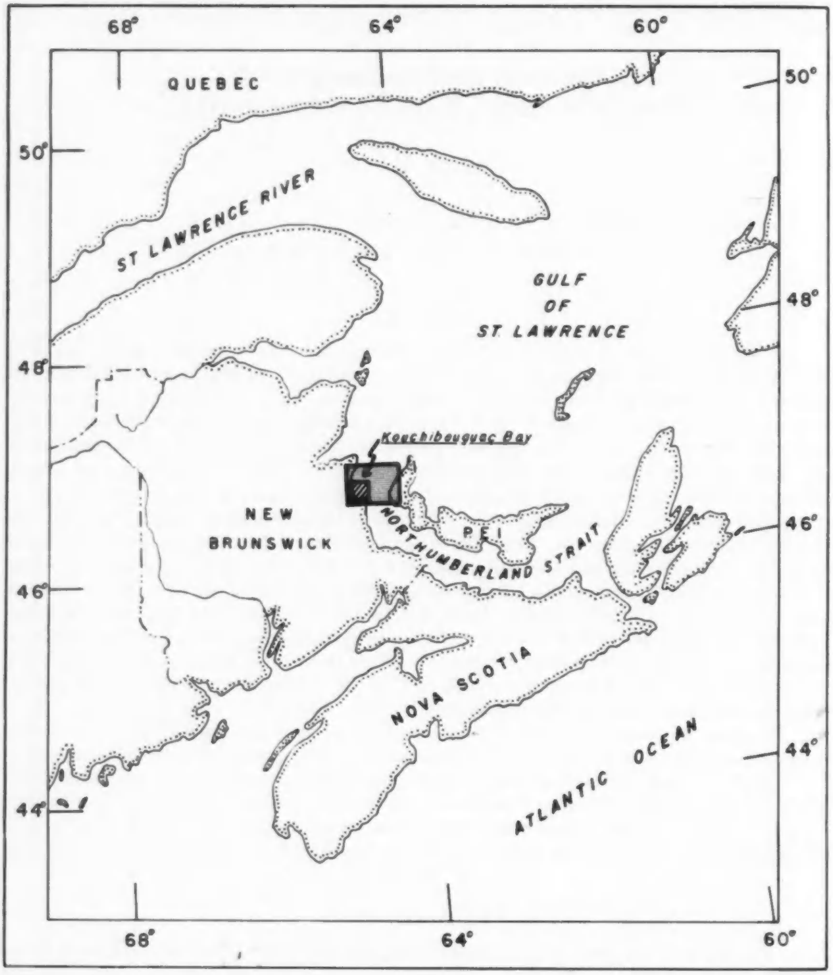

68°
64°
60°
50°
48°
46°
44°
QUEBEC
ST LAWRENCE RIVER
GULF OF ST LAWRENCE
Kouchibouguac Bay
NEW BRUNSWICK
PEI
NORTHUMBERLAND STRAIT
NOVA SCOTIA
ATLANTIC OCEAN

FIG. 1. Index map showing location of study area; Kouchibouguac Bay sample area lined, Northumberland Strait area shaded.

A Van Veen grab-sampler was used to collect the bottom samples. Sampling stations were positioned by means of horizontal sextant angles to known shore positions. Where no sample or only fresh rock fragments were recovered after four attempts, the bottom was assumed to consist of outcrops or very coarse gravel. In the laboratory, size-analyses were performed on the samples using conventional sieve and pipette methods (Kumbein and Pettijohn, 1938). The percentage composition of gravel, sand, and silt of each sample was determined and the Phi Mean diameter, Phi Deviation, and Phi Skewness

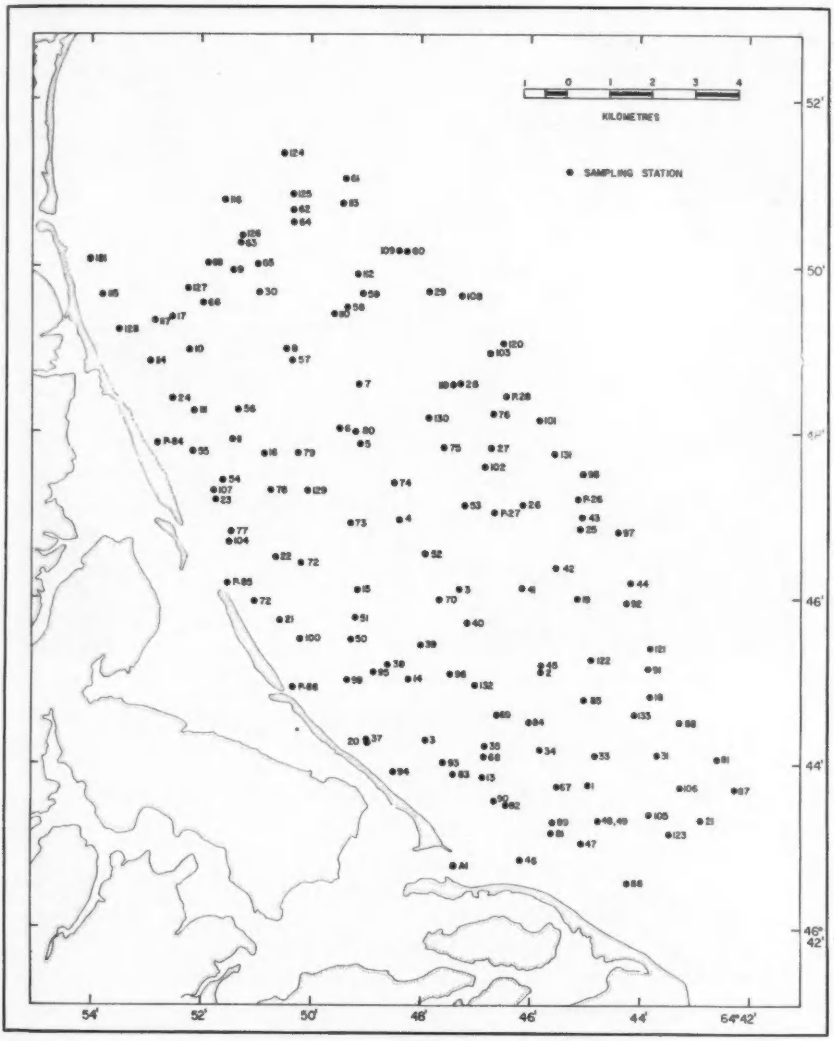

1 0 1 2 3 4
KILOMETRES
SAMPLING STATION
52'
50'
48'
46'
44'
46°
42'
54'
52'
50'
48'
46'
44'
64°42'

FIG. 2. Locations of sample stations in Kouchibouguac Bay.

measure of Inman (1952) calculated for the sandy sediments. Many sandy samples contained a small amount of gravel, commonly in the form of large pebbles. Because this material would have greatly altered the values of the grain-size parameters, the gravel content was excluded in the calculation of sedimentary parameters. This is not an ideal method but is considered an

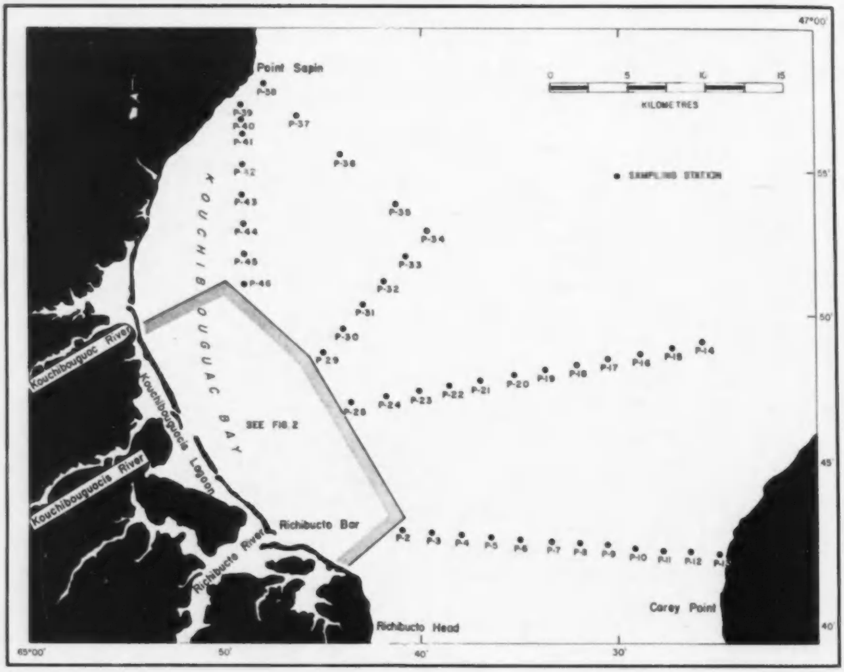

Point Sapin
P-38
P-39
P-40
P-41
P-37
P-36
P-42
P-43
P-44
P-45
P-46
P-35
P-34
P-33
P-32
P-31
P-30
P-29
P-28
P-24
P-23
P-22
P-21
P-20
P-19
P-18
P-17
P-16
P-15
P-14
KOUCHIBOUGUAC BAY
SEE FIG 2
Kouchibouguac River
Kouchibouguacis Lagoon
Kouchibouguacis River
Richibucto Bar
Richibucto River
Richibucto Head
P-2
P-3
P-4
P-5
P-6
P-7
P-8
P-9
P-10
P-11
P-12
Corey Point
0
5
10
15
KILOMETRES
SAMPLING STATION
47°00'
55'
50'
45'
40'
65°00'
50'
40'
30'

FIG. 3. Location of sample station in Northumberland Strait.

essential compromise since many of the samples contain too little coarse material (e.g. one or two pebbles in a well-sorted sand) for it to be representative.

A petrographic examination was made of the gravel and, with the help of thin sections of selected pebbles, the gravel-size particles were classified into four rock-types. The proportion of these rock-types in each sample was determined by pebble counts on the material greater than 4 mm. Samples which consisted of less than five particles were not counted.

Heavy mineral analyses were made of selected samples. The .065–.125 mm fraction was separated by means of bromoform (S.G. –2.89). The separate was split and mounted, and 300–400 grains per slide were identified and counted.

The information obtained from the samples was supplemented by interpretation of echograms of the bottom between stations. From the texture and thickness of the trace, a differentiation was made between a rough bottom composed of rock (bedrock and coarse gravel) and a smooth bottom consisting of sand (Fig. 4).

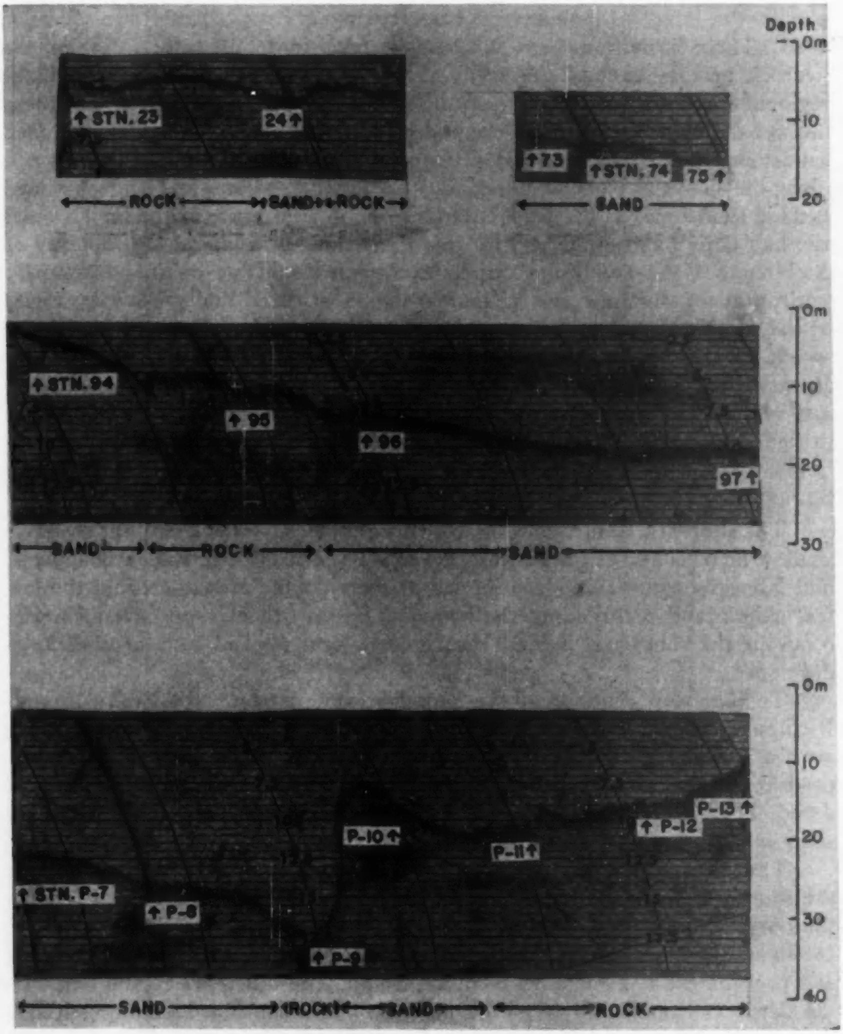


FIG. 4. Examples of echograms showing variations in texture, of different bottom types.

GEOGRAPHICAL SETTING

Kouchibouguac Bay is 32 km (20 miles) long and 9.5 km (6 miles) wide and is situated near the northwestern end of Northumberland Strait, adjacent to the eastern coast of New Brunswick (Fig. 1 and 3).

Physiographically the land around the northern part of Northumberland Strait forms part of the New Brunswick lowlands and is underlain by soft, almost flat-lying, sedimentary rocks of Upper Pennsylvania age (Weeks, 1963). These formations have not been mapped in detail. Information on the bedrock geology around the study area has been derived from generalized regional accounts, and from cursory field observations by the writer. The rocks around the New Brunswick shore consist of green medium- to coarse-grained sandstone, minor clay, and red siltstone of the Pictou group. Most outcrops along the shores of Kouchibouguac Bay are green, medium- and coarse-grained bedded sandstones of the Richibucto formation, and much of the land around the bay is probably underlain by this formation. In a few places, notably at Richibucto Head and Point Sapin, the green sandstone overlies essentially horizontal red siltstone and sandstone with a stiff red and green clay found at the contact. These red beds are thought to be part of the Scouduc formation, which has been described with a similar contact from other parts of New Brunswick (Gussow, 1953). Prince Edward Island consists of red sandstone and siltstone with minor sedimentary rock referred to as Permo-Carboniferous in age.

SHORELINE

The shores of Kouchibouguac Bay are rimmed by sand-bars that separate shallow lagoons and estuaries from the sea. The Richibucto, Kouchibouguacis, and Kouchibouguac rivers are the major rivers in the area and drain the low featureless land surrounding the bay. Off the mouth of these rivers, breaks occur in the sandbars. Behind the lagoons, swamps and salt marshes have developed.

To illustrate changes in the shoreline and bottom topography around Richibucto Bar during the last 125 years, a series of maps have been drawn on the basis of hydrographic charts dating back to 1839. Five maps are reproduced that show the shoreline and bottom contours according to surveys dated 1839, 1894, 1930, 1959, and 1964 (Fig. 5). Comparison of these maps show a sequence of changes in the physiographic configuration of the area.

The most significant development in the history of Richibucto Bar is the southeast longshore migration of North Beach, the sand spit which forms the northern part of Richibucto Bar. This change is extremely clear between 1839 and 1964 during which time a breakwater was built to stop this process and prevent the river channel from silting up. The difference in the shape of the spit in 1894 and 1930 shows this process to have continued and necessitated further construction of breakwaters. By 1959 longshore movement of sand had caused deposition behind the whole pre-1930 breakwater. Accompanying and related to this process is the development of the underwater bar east of the North Beach barrier. Although too much emphasis must not be put on the values of the soundings of the older maps because of uncertainty in the method used in correction of tidal heights, the submarine contours do show a distinct eastward lengthening of the underwater bar. This indicates the existence of a southeastwardly longshore current that transports and deposits sand to the area of the bay.

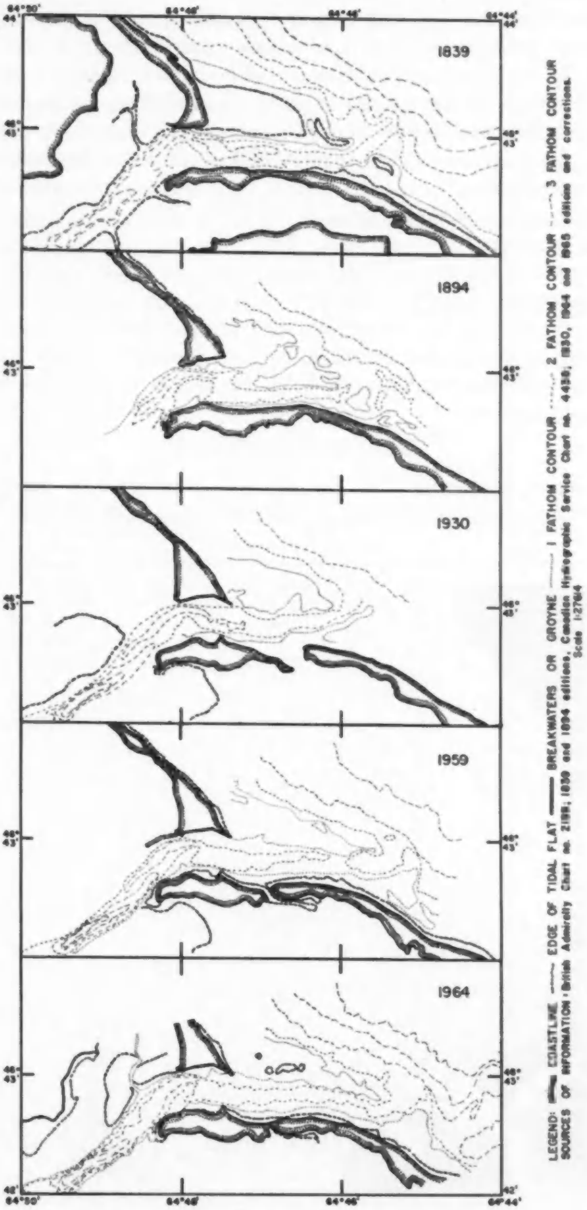

64°50'
64°48'
64°46'
64°44'
46°44'
46°43'
46°42'
1839
1894
1930
1959
1964
LEGEND: COASTLINE EDGE OF TIDAL FLAT BREAKWATERS OR GROYNE 1 FATHOM CONTOUR 2 FATHOM CONTOUR 3 FATHOM CONTOUR
SOURCES OF INFORMATION: British Admiralty Chart no. 2198; 1839 and 1894 editions, Canadian Hydrographic Service Chart no. 4426; 1930, 1964 and 1965 editions and corrections.
Scale 1:27664

FIG. 5. Maps of Richibucto Bar and environment drawn after hydrographic charts from 1839 to 1964 showing changes in shoreline and bottom topography.

The existence of a southeast flowing current is indicated by data obtained by Blackford (1965) from a current meter placed about 2½ miles north off North Beach. During the one month for which complete water transport data was available a net southeastward longshore movement of water occurred. By 1964 parts of the underwater bar had become a tidal flat and, eventually, the whole bar will probably build up above water as a sand barrier.

A slight widening of South Beach, the southern barrier spit forming Richibucto Bar has taken place since its 1894 width. This growth was most pronounced between 1839 and 1894. After this time South Beach appears to have stabilized, probably as North Beach was extended and longshore drift bypassed the more protected southern shore of the channel. Between 1894 and 1930 a rupture of the south barrier occurred, probably as a result of a sudden storm accompanied by high waves. The subsequent maps show a gradual closing of this break and in 1964 the southern shoreline had regained its 1894 configuration.

BOTTOM TOPOGRAPHY

The bottom topography of the northwestern part of Northumberland Strait (Fig. 6) is drawn on the basis of published and unpublished hydrographic

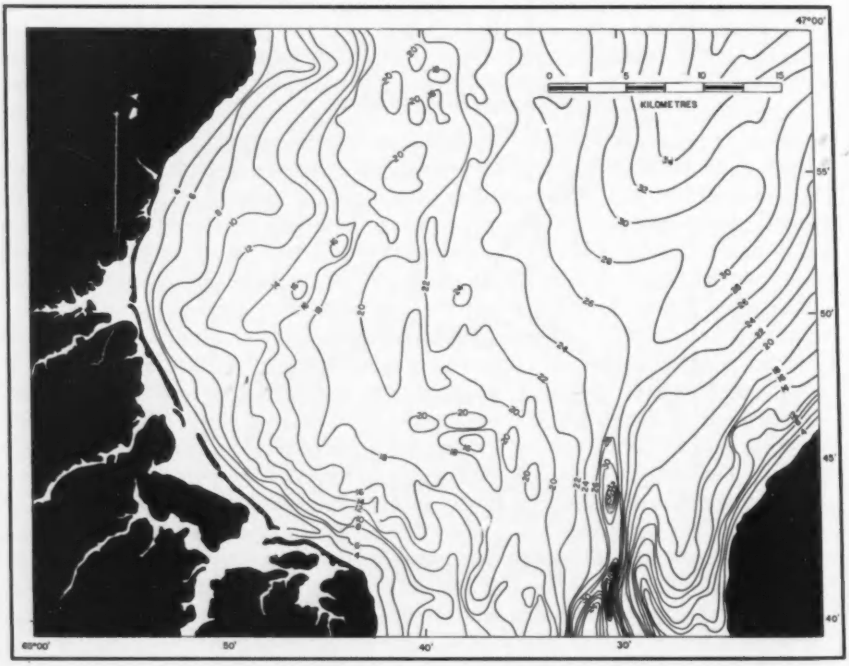


FIG. 6. Submarine topography of northwestern part of Northumberland Strait showing submarine trough off the western end of Prince Edward Island. Depths in meters.

charts and sounding traces obtained during the field work. The topography of the detailed sampling area is shown in Fig. 7. Except for the area of Richibucto Bar, based on the Richibucto Harbour chart (No. 4438), this map is based entirely on sounding lines obtained during the present field work. The information is subject to errors in positioning and the data have not been corrected to Mean Sea Level Datum.

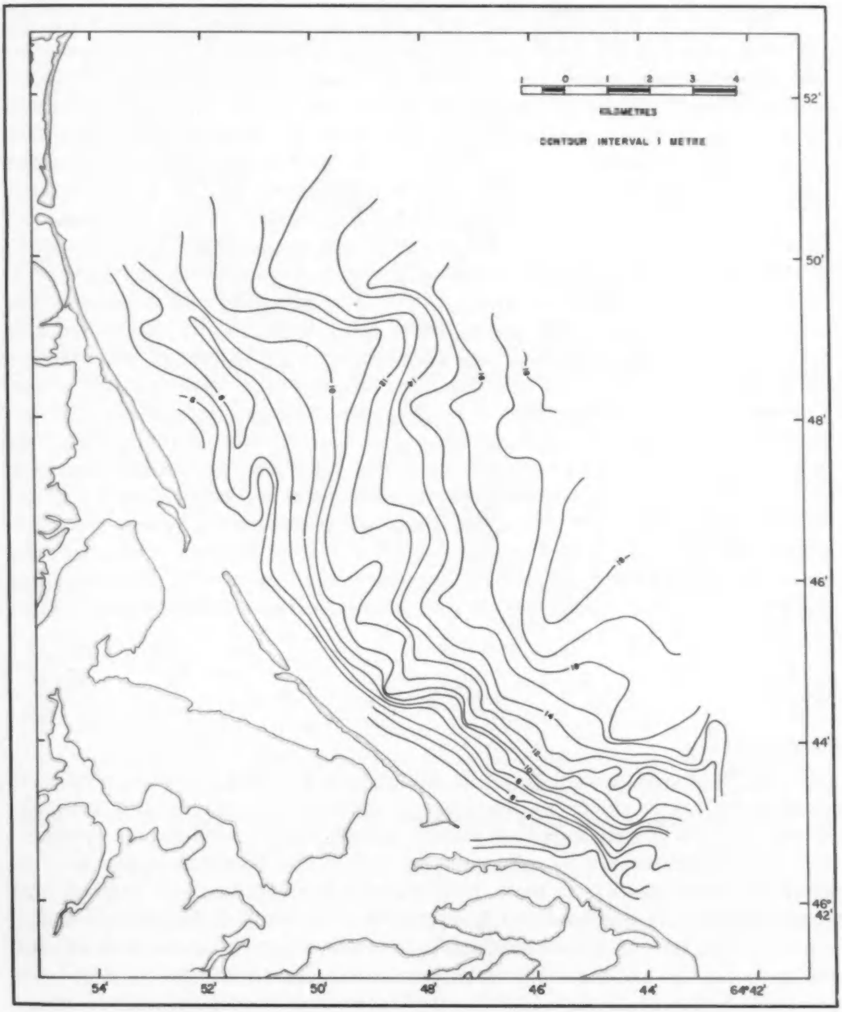

1 0 1 2 3 4
KILOMETRES
CONTOUR INTERVAL 1 METRE
52'
50'
48'
46'
44'
46°
42'
54'
52'
50'
48'
46'
44'
64°42'
14
12
10
4

FIG. 7. Submarine topography of southern part of Kouchibouguac Bay.

The bottom of Kouchibouguac Bay slopes gently from the shore to a depth of about 18 m near the limit of detailed mapping. Two roughly triangular-shaped ridges, or benches, about 10 km wide extend outward from the land and contrast with the smoother topography of the bay. Near the headlands of the bays, the bottom slopes more steeply seaward and within 10 km deepens to 18 m. The bottom of the central part of the Strait deepens towards the middle and is relatively flat and featureless except for two areas of hummocks and depressions of probable glacial origin.

The bottom near Prince Edward Island contrasts with the rather featureless topography of the western side of the Strait. About 15 km from the western end of the island, a 3–5 km wide trough occurs. It is oriented in a north–south direction and forms the deepest part of the Strait. The trough averages about 25 m in depth, and is 6–8 m deeper than the general level of the floor of the Strait. Opposite Carey Point, P.E.I., the trough branches into two parts extending southward. The narrow continuous nature of the trough, the general U-shaped cross section, and the division into two branches may indicate that the trough represents an old drainage channel from a lower stand of sea level. On the bottom of the trough, two depressions with depths to 36 m occur. These depressions are about 1 mile long and about 1½ miles from one another. They resemble the pater noster lakes produced by glacial scour in a confined channel, and may have resulted from the action of glaciers in a former river channel. The sides of the troughs are asymmetrical in shape. The slope of the western side is fairly gentle whereas the eastern side has steep, in places almost vertical, sides. The eastern side of the trough rises to a depth of 2 m and forms the ridge called West Reef on the Hydrographic Charts. This ridge curves towards the southeast and is connected to the Prince Edward Island mainland by means of a shallow platform. Towards the north around 65°47′ latitude the trough loses its narrow confined character and widens northeastward into a broad depression, and eventually joins the large shallow basin which forms the bottom where Northumberland Strait widens into the Gulf of St. Lawrence.

BOTTOM TYPES

INTRODUCTION

The dominant bottom types in Kouchibouguac Bay based on geological composition are medium- to fine-grained sand, coarse gravel, and bedrock. Minor amounts of silty sand and poorly sorted gravelly sand are also present. Figure 8 illustrates the sample composition in the Kouchibouguac area in terms of gravel, sand, and mud. It shows samples composed of bedrock and gravel to occur closely associated, surrounded by areas of dominantly sandy sediment. The nature of the bottom as interpreted from echograms is illustrated in Fig. 9. On the basis of these two maps a generalized bottom lithology map has been constructed (Fig. 10). On this map four lithological bottom types have been distinguished; bedrock, gravel, sand, and mixed sand and gravel.

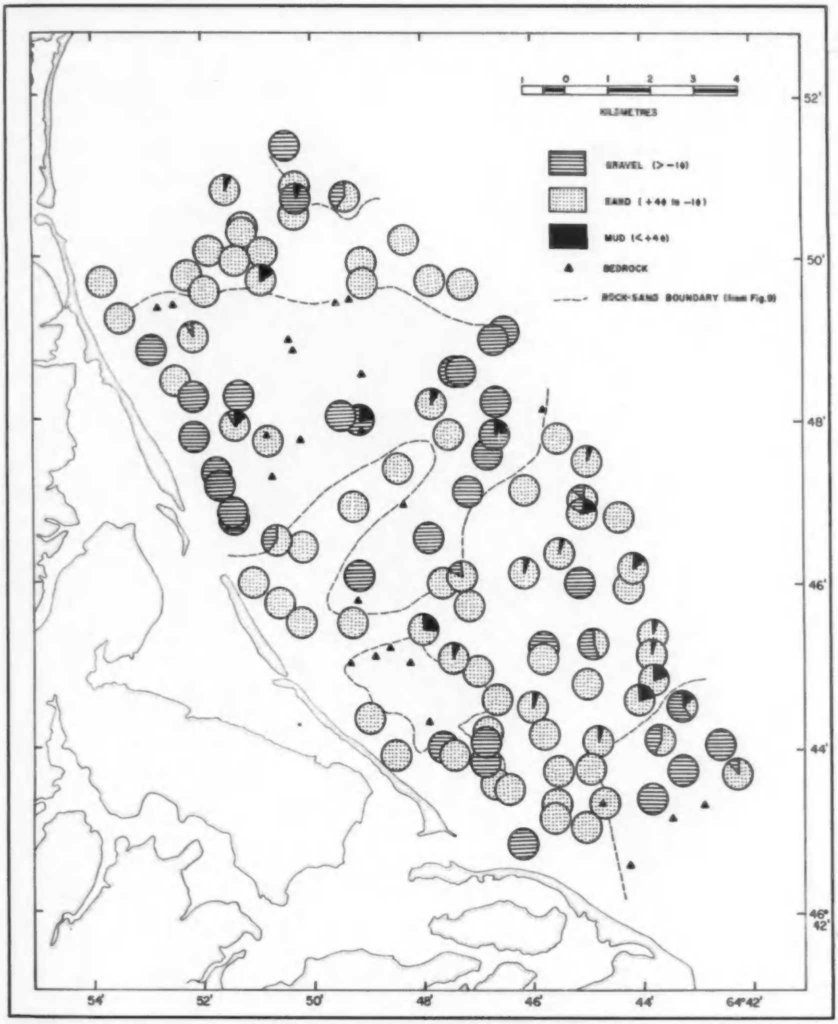

1 0 1 2 3 4
KILOMETRES
GRAVEL (> −1φ)
SAND (+4φ to −1φ)
MUD (< +4φ)
BEDROCK
ROCK-SAND BOUNDARY (from Fig.9)
52'
50'
48'
46'
44'
46° 42'
54'
52'
50'
48'
46'
44'
64°42'

FIG. 8. Textural composition of samples from Kouchibouguac Bay showing concentration of bedrock and gravel in three areas.

Different lithological types occur closely associated and intermixed and therefore, distinct lines drawn between them are sometimes arbitrary.

The striking feature of the bottom of Kouchibouguac Bay is a roughly triangular-shaped area of gravel and rock. The central part of this feature consists of bedrock but near the shore and western edge, gravel is dominant.

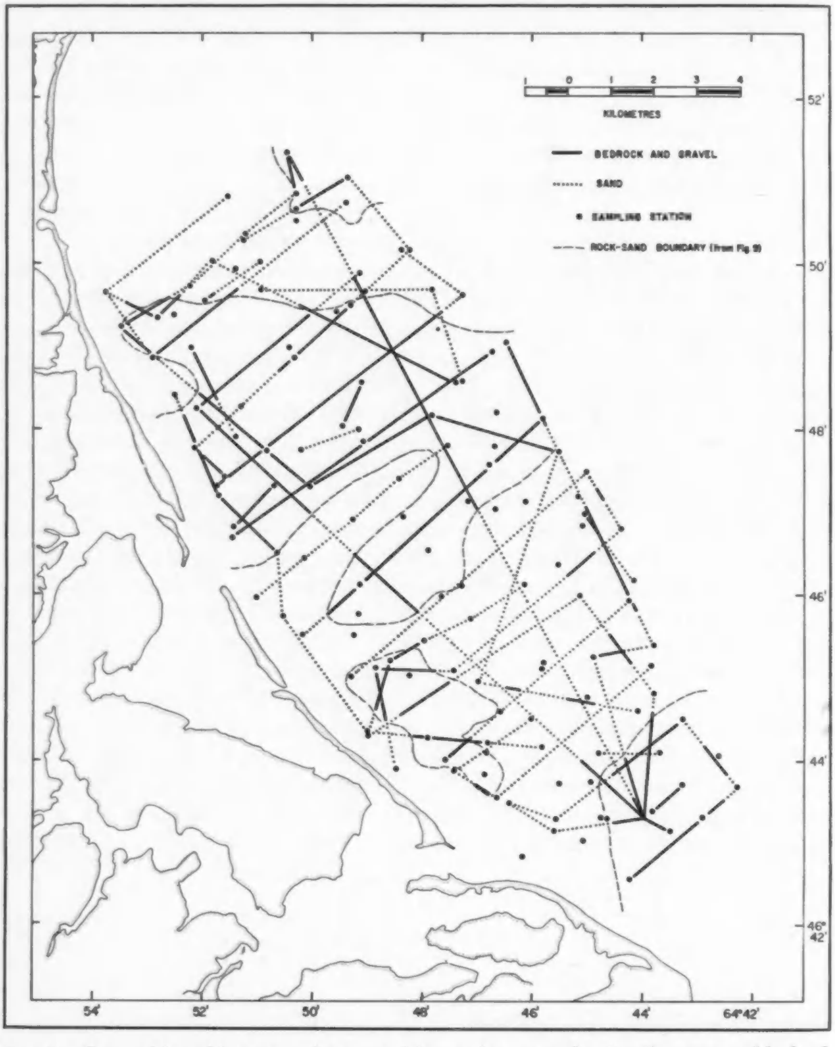

1 0 1 2 3 4
KILOMETRES
BEDROCK AND GRAVEL
SAND
SAMPLING STATION
ROCK-SAND BOUNDARY (from Fig. 8)
52'
50'
48'
46'
44'
46°
42'
54'
52'
50'
48'
46'
44'
64°42'

FIG. 9. Composition of bottom as interpreted from echograms, showing three areas of bedrock and gravel. Dotted and solid lines represent tracks over bottom. For location of stations see Fig. 2 and 3.

A tongue of sand transects the area and another strip of sand divides a narrow extension of bedrock and gravel north of Richibucto River mouth from the central area. Sand as well as mixed sand and gravel separate the central rocky area from two smaller areas of bedrock; one at the northern, and one at the southeastern corner of the sample area. The oblong stretch of mixed gravel,

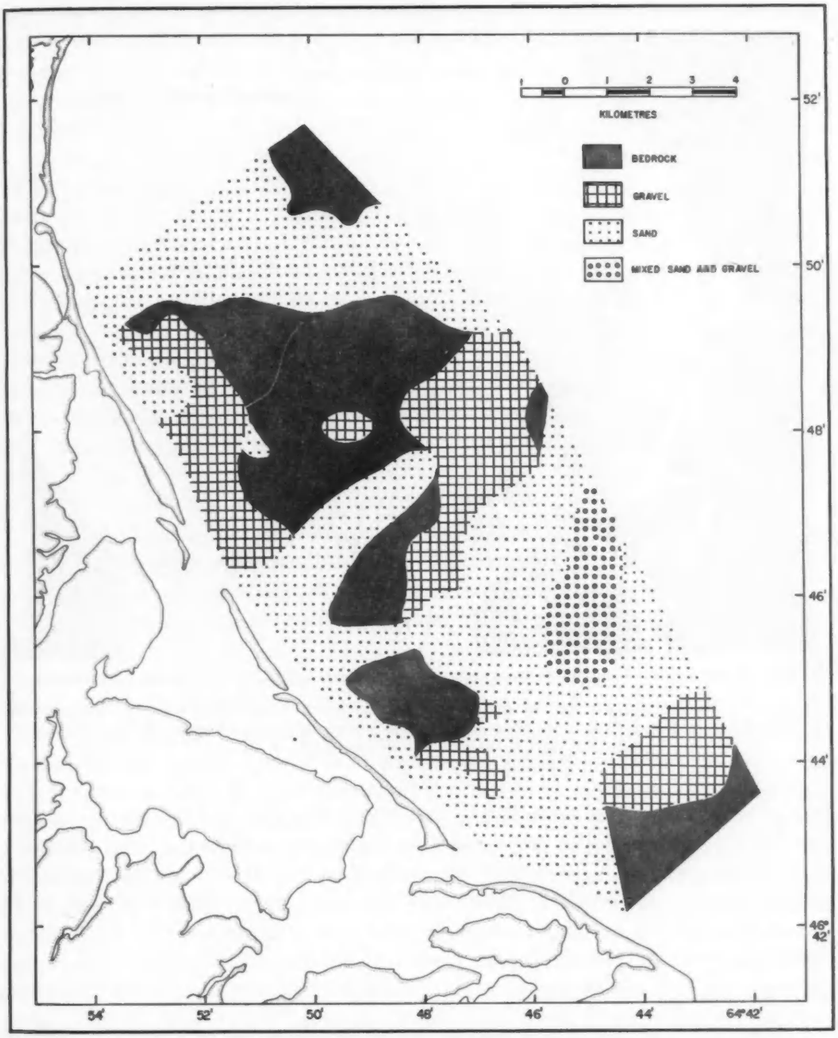

1 0 1 2 3 4
KILOMETRES
BEDROCK
GRAVEL
SAND
MIXED SAND AND GRAVEL
52'
50'
48'
46'
44'
46° 42'
54'
52'
50'
48'
46'
44'
64°42'

FIG. 10. Bottom lithology of the southern part of Kouchibouguac Bay drawn on the basis of sediment composition (Fig. 7) and echograms (Fig. 8).

sand, and silt in the south-central part of the sample area is distinguished from the other gravel because of its poorly sorted nature and the lack of associated bedrock.

A comparison of Fig. 8 and Fig. 11 shows a distinct relationship between topography and lithology. Areas of bedrock and gravel correspond to topographic highs, and areas of sand coincides with topographic lows. The central

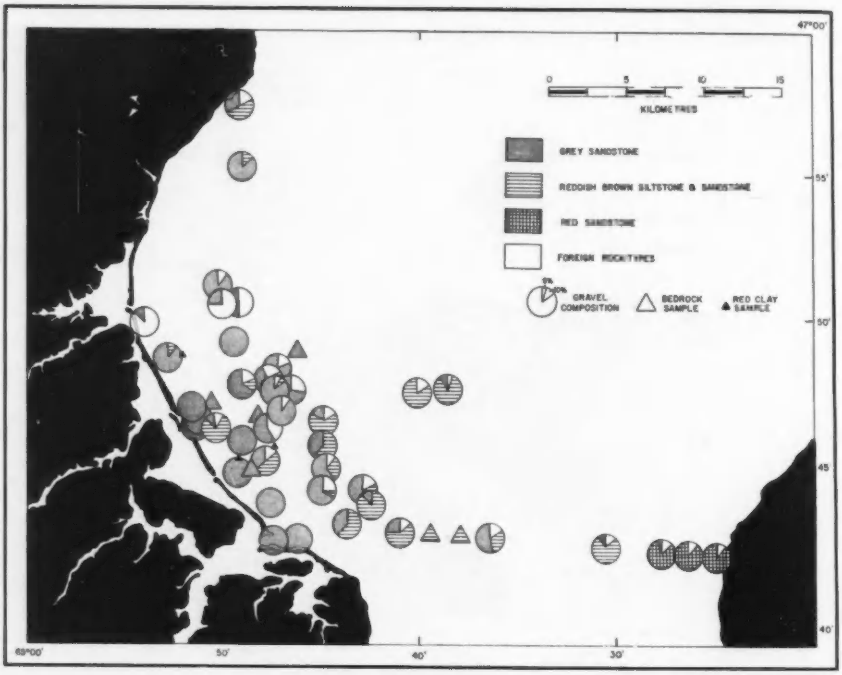

47°00'
55'
50'
45'
40'
65°00'
50'
40'
30'
0
5
10
15
KILOMETRES
GREY SANDSTONE
REDDISH BROWN SILTSTONE & SANDSTONE
RED SANDSTONE
FOREIGN ROCKTYPES
0%
10%
GRAVEL COMPOSITION
BEDROCK SAMPLE
RED CLAY SAMPLE

FIG. 11. Petrologic composition of gravel-size sediments in Kouchibouguac Bay and Northumberland Strait area showing change from grey to reddish-brown sediments off Kouchibouguac Bay and red sandstone off Prince Edward Island.

area of rock and gravel covers the large bench or ridge in the central part of the sample area, and the smaller rocky areas are expressed topographically as subdued benches. Generally the areas of rocky terrain have a rougher surface and are elevated in relation to the more featureless sandy bottom.

BEDROCK AND GRAVEL

TEXTURE

About 40% of the sample area in Kouchibouguac Bay consists of bedrock, or bedrock covered by minor gravel (Fig. 10). From a few stations, samples of the bedrock were recovered (Fig. 9). These outcrop specimens consist of angular rock fragments with one or more fresh faces. They were usually recovered after several attempts to obtain a sample in areas where no sediment samples were obtained.

The gravel size material occurs as a large variety of textural types. It is found both as a clean, coarse gravel and as a poorly sorted sediment mixed with sand or sand and mud. Lack of textural homogeneity makes it difficult to draw any definite boundaries between the different types. The gravel varies from angular to well rounded. In general, angular pebbles occur associated with a poorly sorted sediment that contains a substantial amount of mud whereas better rounding is displayed by clean gravel and sandy gravel. The gravel found in the study area is too coarse to have been transported to its present depth by marine hydraulic agents and must be relict material from an earlier environment. The wide range of grain size, lack of rounding of particles, and presence of foreign rocks shown by the poorly sorted, muddy, sandy gravel are all characteristics of glacial till. This sediment was probably deposited by Pleistocene glaciers. The samples composed only of sand and gravel probably have a similar origin but have been reworked by wave and current action subsequent to deposition. This has resulted in rounding of the gravel size material and removal of some or all of the fines. With the clean gravel this process has gone further and only a lag deposit of coarse gravel remains. In order to round the cobble-sized particles, fairly vigorous wave action would be required. This is most likely to have occurred in the surf zone of a beach and at a lower sea-level than the present.

COMPOSITION

With the help of petrographic examination of thin sections, bedrock and gravel samples were studied and compared with the rocks that outcrop along the shores of the Bay. From the bedrock samples as well as from the gravel some indication of the composition of the underlying bedrock may be obtained.

The composition of the bedrock samples and gravel fragments larger than 4 mm is illustrated in Fig. 11.

Four of the six bedrock samples recovered consisted of a medium- to coarse-grained, greyish-green sandstone. The dominant grains are quartz, rock fragments, feldspar, and mica and the heavy minerals include hematite, magnetite, zircon, tourmaline, garnet, amphibole, and pyroxenes. The sandstones are characterized by a great abundance of rock fragments, which consist principally of slates and schists with lesser amounts of volcanic rocks and are classified as sub-greywackes (Pettijohn, 1957). Much of the quartz occurs in the form of compound grains such as fine-textured quartzite and chert. Calcite is the principal cementing agent of the medium- and coarse-grained sandstone, whereas iron oxide and quartz forms the cement in the finer-grained rocks. These grey sandstone samples are similar to the sandstones of the Richibucto formation exposed in numerous outcrops along the shores of Kouchibouguac Bay, and indicate that rock of this formation underlies the bay.

Two samples of a reddish-brown siltstone were obtained. This material has much the same composition as the grey sandstone, and no differences could be detected in the heavy mineral suite. The red colour is due to iron-oxide cement and an abundance of oxidized rock fragments. The samples of this rock type come from stations outside the headlands of Kouchibouguac Bay, about 2 miles northeast of Richibucto and are probably derived from the Scouduc formation. Beds of this formation of similar lithology outcrop near the headlands of the bay at Richibucto Head and Point Sapin and may be assumed to underlie some of the bottom outside Kouchibouguac Bay.

When sampling the study area, a stiff red clay with patches of blue clay was recovered in three places. Thin sections of dried samples of this material show it to consist of a mixture of clay minerals and fine-grained carbonate minerals with fine-grained iron-oxide minerals throughout. At two of the three stations where this material was collected the clay sample was brought up adhering to the anchor, whereas only clean sand was obtained with the grab-sampler. The texture and colour of this clay is identical to the red and green clay that forms the boundary between the Richibucto and Scouduc formations. Therefore the red clay horizon, and probably also the underlying Scouduc "red beds" occur beneath a thin veneer of sand in depressions within Kouchibouguac Bay. Beds of the Richibucto formation are probably very thin and in places discontinuous. This is to be expected because the contact between the two formations can be observed along the outer shores of the bay at Point Sapin and Richibucto Head.

Additional information about the bedrock underlying the study area may be gained from the composition of the gravel fraction (Fig. 11). Since most of the gravel in this area is glacial material or reworked glacial material, it can be assumed to have a composition related to the underlying bedrock (Goldthwait, 1924; Lundquist, 1935). From petrographic studies the gravel-size particles have been classified into four rock types: (1) greenish-grey sandstone: (2) reddish-brown sandstone and siltstone: (3) red sandstone: and (4) foreign rock types. The first two groups are identical in texture and mineralogy to the local rock types discussed above and are assumed to have been derived from these formations. In three samples taken from stations near the Prince Edward Island coast particles of red, coarse-grained sandstone were found. This material is lighter in colour and better indurated than the reddish-brown rock of the Scouduc formation. Some of these particles contain abundant mudstone pebbles and may be termed mudstone conglomerate.

The foreign rock types include rock types not found along the shores of the sample area and consist of glacial erratics and probably also some material ice-rafted into the area. These foreign rock types are: slates, quartzite, limestone, volcanics, and greywacke, in order of abundance. The most likely source appears to be the highlands of New Brunswick, where all these types are known to occur (Weeks, 1963). Some of them in particular the limestone, may also have been ice-rafted from the Gaspé region or from areas farther north.

Green sandstone was the dominant rock type in most samples from the inner part of Kouchibouguac Bay, which suggests that this part of the bay is underlain by the Richibucto formation. Seaward of a line which joins the headlands of the bay the red siltstone becomes more abundant. This is probably a reflection of the composition of the underlying bedrock. Two samples with high percentages of brown siltstone also occur inside the bay and indicate that the Scouduc beds come to the surface as shown by the presence here of red clay. Thus the areal distribution of gravel composed of the green sandstone, and the distribution of red sandstone and siltstone within the bay supports these conclusions reached from the study of bedrock samples.

The red sandstone found near the coast of Prince Edward Island differs from the Scouduc rocks in respect to colour, texture, and grain size and is probably derived from the sediments underlying the island. The distinct difference in composition of the sediment on two sides of the deep trough off Prince Edward Island is noteworthy. Samples containing red sandstone were collected east of the trough whereas the samples on the western side consisted of brown siltstone and light-brown sand. This indicates a geological boundary along the trough. The eastern edge of the trough may be formed by a ridge of younger more resistant rock of the Prince Edward Island rocks. This would account for the asymmetrical shape of the trough.

SAND

TEXTURE

Sand covers about one-half of the nearshore sample area and forms one of the dominant sediment types in the Northumberland Strait samples. Gravel-size material is found in some of the sand samples but most of the sand is well sorted and forms one of the most homogeneous and wide-spread bottom types in the area.

The phi mean diameter of sand-size sediments ranges from 3.90 ϕ to 0.80 ϕ, sorting values from 0.16 to 1.22, and skewness from +.38 to −.53 (Inman, 1952). The distribution of mean diameter and skewness is illustrated in Fig. 12 and 13. In studying the areal distribution of these parameters those samples without gravel and composed of less than 16% silt and clay were used. When samples are analyzed by a combined sieve–pipette method, a change in the slope of the cumulative curve commonly occurs at the sand–silt boundary (4 ϕ) as a reflection of the change from sieve to pipette method of analysis. In deriving Inman measures the ϕ 84 and ϕ 16 percentiles are used and consequently in samples composed of more than 16% mud, the ϕ 84 percentile will fall within the portion of the curve based on pipette analysis. Therefore such samples will not yield statistical values directly comparable to those derived from a straight sieve analysis and such samples were not utilized in construction of Fig. 12 and 13.

In the initial plotting of the sedimentary parameters, samples containing gravel were included but were found to have anomalous values in relation to the distribution pattern as a whole. This may indicate that the gravel is an integral part of the sample, and removal of this portion in the calculation of the statistics distorts the natural characteristics of the distribution. These gravelly samples may also have a different origin from the clean sand, and may not have had time to adjust to the environmental factors that control the texture of the latter. Such a condition might be expected if sand deposited by modern hydraulic agents occurs associated with reworked glacial material.

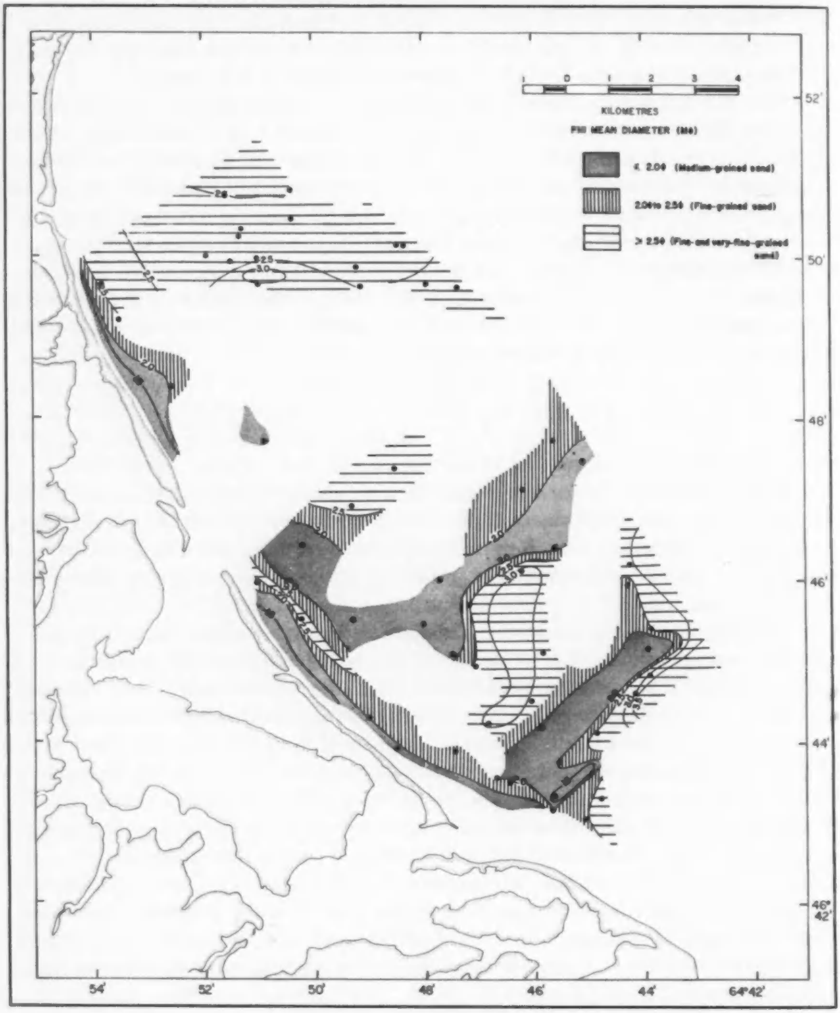

1 0 1 2 3 4
KILOMETRES
PHI MEAN DIAMETER (Mφ)
< 2.0φ (Medium-grained sand)
2.0φ to 2.5φ (Fine-grained sand)
> 2.5φ (Fine- and very-fine-grained sand)
52'
50'
48'
46'
44'
46° 42'
54'
52'
50'
48'
46'
44'
64°42'
2.5
3.0
2.0

FIG. 12. Phi mean diameter of sand in Kouchibouguac Bay showing coarse-grained sand along the shore and three anomalies of coarse-grained sand crossing the sample area perpendicular to the shore, surrounded by finer-grained sand. Dots show location of samples used in complication of map.

The mean diameters of the sand samples show a distinct pattern within the Kouchibouguac sample area as shown by the contoured values in Fig. 12. From the shore outwards across a 1-mile zone, a regular decrease in grain size from 1 ϕ to around 3 ϕ occurs. This northwest–southeast trending distributional

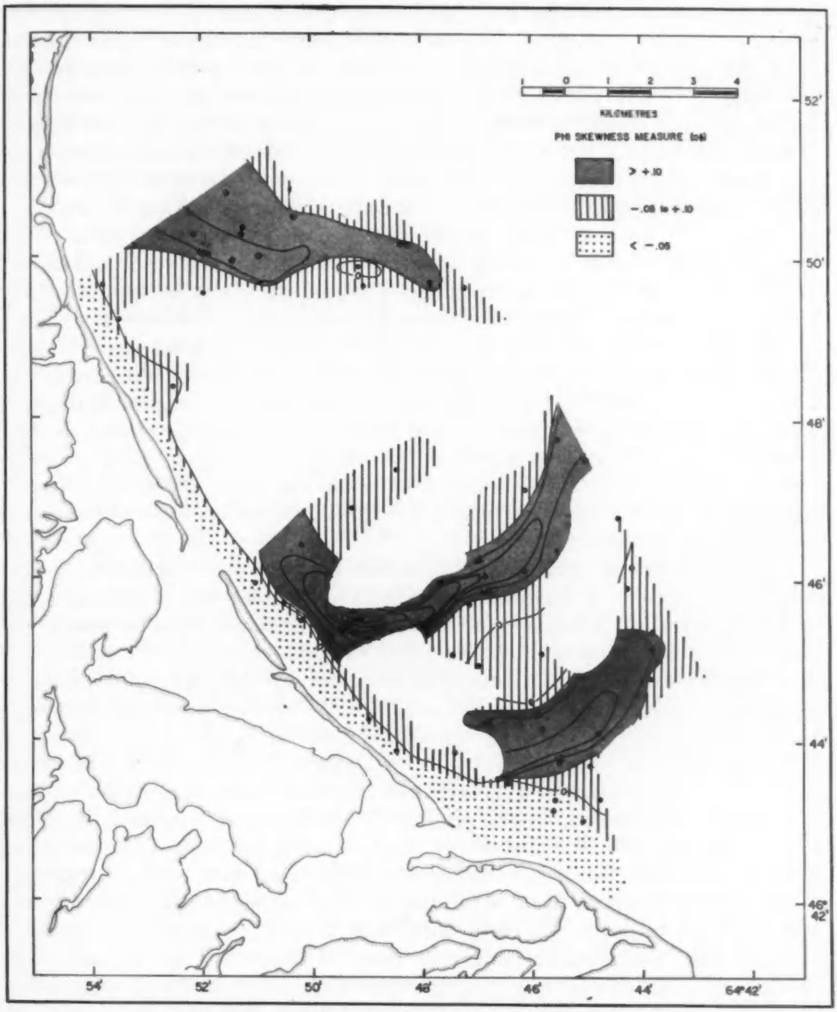

1
0
1
2
3
4
KILOMETRES
PHI SKEWNESS MEASURE (αφ)
> +.10
−.08 to +.10
< −.08
52'
50'
48'
46'
44'
46°
42'
54'
52'
50'
48'
46'
44'
64°42'

FIG. 13. Phi skewness measures of sand in Kouchibouguac Bay showing zone of negatively skewed sand along the shore and three anomalies of positively skewed sand crossing the sample area perpendicular to the shore, surrounded by neutrally skewed sand. Dots show location of samples used in compilation of map.

pattern contrasts with a northeast–southwestward distribution prevailing in deeper waters. In the deeper part of the bay a series of elongated bodies, approximately 1 mile wide, of coarse-grained sand extend from the edge of the nearshore zone to the outer boundary of the sample area. These bands are surrounded by sand of finer grain size, and are separated from one another by a ridge of bedrock and gravel. The shoreward ends of the elongated sand bodies lie in the vicinity of the openings in the offshore bars opposite the mouths of the major rivers in the area. No distinct distributional pattern is shown by the sorting (dispersion) measures. A slight decrease in sorting seaward appears to exist in some areas but in general the sorting values are randomly distributed. The distributional pattern of the skewness values is very similar to that shown by the mean diameter. Along the shore a zone of negative values with skewness of −.05 to −.10 occurs. In the deeper waters positive values (+.10 to +.80) form three southwest–northeast trending bands that extend perpendicular to the coast from the barrier openings to the edge of the sample area. The intermediate areas of sand have skewness values close to neutral (−.05 to +.10). A comparison of the maps (Fig. 12 and 13) illustrating mean diameter and skewness shows a close relationship between the two textural parameters. The longshore area of high mean diameter corresponds to the zone of negative skewness, whereas the offshore bands of coarser mean diameter almost coincide with the areas of positive skewness values. The remaining sand possesses neutral skewness and smaller values of mean diameter. Thus a pattern is produced of three sand types which are distinguished on the basis of mean diameter and skewness.

Several workers have investigated the relationship of sedimentary parameters to depositional environment and have concluded that certain measures are environmentally sensitive and indicative of certain hydraulic conditions. Mason and Folk (1958), Friedman (1961, 1962), Duane (1964), and others have shown that mean diameter and skewness are useful in differentiating depositional environments such as beach, dune, and river sands. Skewness measures calculated on the basis of moment measures or the graphic measures of Inman (1952) or Folk and Ward (1957), yielded negative values for beach or littoral zone sediments whereas most dune and river sands were found to be positively skewed. Friedman (1961) attributes the negative skewness of beach sediments to the winnowing action of waves, and the positive skewness of river and dune sands to transportation by unidirectional current flow, which result in an upper size limit to the material carried in suspension. Duane (1964) relates negative skewness with high energy environments, positive skewness with low energy levels, and areas characterized by no particular dominance of positive or negative skewness with areas of fluctuating energy levels. The above workers found no distinguishing numerical limits in mean size for the sedimentary types studied, but in connection with other parameters it helped to differentiate environments. This is to be expected as the mean size of a sediment is related to the velocity of the transporting current (Hjulström, 1939). Thus both the mean diameter and skewness characteristics of sediments may be used as guides to the character and strength of the hydraulic environment that have produced the sediments. Three types of sand in Kouchibouguac Bay, as defined above on the basis of mean diameter and skewness, appear to reflect three distinct sets of hydraulic conditions: (1)

the negatively skewed, medium-grained sands are in agreement with values reported for beach and littoral sediments subject to vigorous reworking by wave action; (2) the positively skewed, relatively coarse-grained sand may be the result of unidirectional currents with high energy and transportation competence; and (3) the relatively fine sand with mixed positive and negative skewness may be the product of deposition in less turbulent water with a less distinct current pattern.

Two processes that might produce a flow across the outer part of the sample area perpendicular to the shore are rip currents and out-flow of river water. Rip currents, the process by which water carried towards shore by waves is returned seaward, has been studied in detail along an open sandy shore by Shepard and Inman (1950). The position of these rip currents is dependent on submarine topography and configuration of the coast and on the height and period of the waves. However, the dimensions of the sand bodies as outlined in Fig. 12 and 13 are larger than would be expected to have been formed by rip currents in Kouchibouguac Bay. Another feature of rip currents is periodicity, or fluctuation of current velocity and direction, whereas the positive skewness of the sand anomalies in the sample area indicates that a steady permanent current affects the areas. The shoreward end of the anomalies occurs near one of the major rivers draining into the bay. This association suggests that river flow may be responsible for the present sand distribution. However, the freshwater that flows into the bay is more likely to spread out on top of the denser salt water as a diffuse mass rather than continuing seaward as a distinct current, and moreover it is unlikely that the debouching river water would have retained much sediment after flowing across the lagoons which would act as catchment basins. Also, at the present time the sand anomalies are somewhat offset from the mouths of major river channels.

The positive skewness of the sand bodies and their proximity to present river mouths, may indicate that the sand anomalies are relict river-channel deposits. Any sedimentary parameters as sensitive as skewness would normally have been obliterated in the surf zone as the shoreline passed over the area. However, if the rivers flowed into the bay through a channel that remained below the effective depth of breaking waves, a relict distributional pattern could have been preserved and would now mark the location of former river channels. At the present time the location of the sand anomalies are offset relative to the barrier openings. Offshore barriers are usually considered to be formed as longshore spits by the action of longshore drift during submergence of lowland coasts (Shepard, 1963, p. 187–192). Studies of shoreline changes by means of old hydrographic charts show a southeastward migration of North Beach (Shepard, 1963, p. 10–11). The barrier bars in Kouchibouguac Bay may have been superimposed across earlier river channels and thereby have caused the river mouths to be shifted to their present position.

The abrupt truncation of the offshore pattern of distribution by the narrow sand zone along the shore with a normal sequence of decreasing grain size towards deeper water further indicates that the sediments that form the offshore distribution pattern are relict from a former sea level.

In a study of current circulation in Kouchibouguac Bay, Blackford (1965) found shoreward movement of water near the bottom. This process probably prevents sediment from the barrier bars from being deposited in the offshore area. A net shoreward movement of sand may occur which helps to keep exposed any relict patterns of sediment distribution. In order to determine conclusively the origin of the offshore sand anomalies more work is required in the area including further sampling, more detailed analysis using $\frac{1}{4}$ ϕ sieve intervals, and detailed current measurements.

COMPOSITION

Petrological analysis of the composition of the sand-size sediments was limited to heavy mineral analysis of selected samples representative of the study area. Three dominant grain types in the heavy fraction are: rock fragments, iron-oxide coated grains, and metallic minerals. The rock fragments consist of a large variety of rock types similar to grains observed in thin sections of samples obtained from the local sedimentary formations. No attempt was made to classify these rock fragments. Iron-oxide coated grains include a wide variety of minerals. The abundance of these grains is related to the

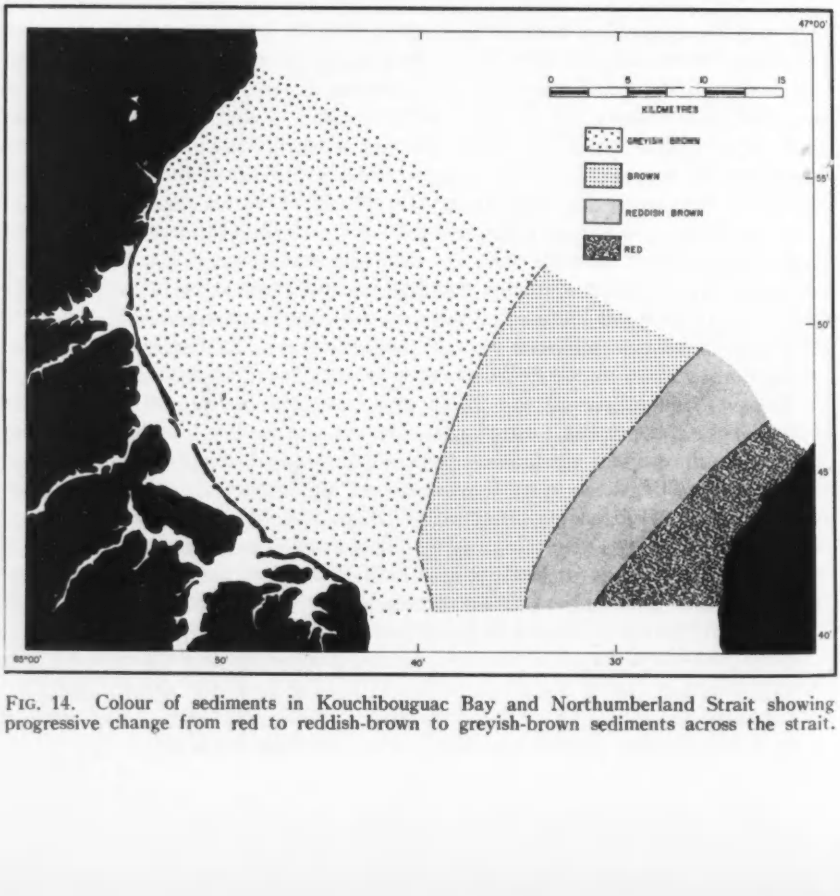


FIG. 14. Colour of sediments in Kouchibouguac Bay and Northumberland Strait showing progressive change from red to reddish-brown to greyish-brown sediments across the strait.

TABLE I.

Sample No.	36	46	63	70	71	74	97	98	109	125	P–6	P–10	P–12	P–13	P–22	P–31	P–37	P–39	P–43
Rock fragments	41	14	56	53	50	49	10	27	25	5	17	18	29	13	16	35	19	30	22
Metalic minerals	23	42	16	16	15	23	13	20	37	41	60	41	38	45	41	13	52	35	40
Iron-oxide coated grains	10	17	14	18	6	5	39	14	7	5	10	27	10	27	15	26	2	8	27
Zircon		4		+	+	+	+	+	2	6	2	+	3	2	+	+	9	3	+
Tourmaline	+		3	+	+	+	2	+	2	+	+	2	+	+	+	+		3	+
Monazite							+			+	+			+			+	+	+
Apatite	+	+			+	+			3	+	+	+	3	+				+	+
Epidote	+						+		+		+		+		+			+	
Garnet	2	4	2	5	+	4	5	7	4	3	6	2	4	2	6	1	7	6	2
Andalusite	6	4	5	2	+	7	5	9	7	3	+	+	5	3	5	+	+	3	+
Hornblende	4	3	2	2	+	7	7	14	7	4	+	+	+	+	+	2	+	5	+
Actinolite		+	+				+		+	+			+	+		+			
Tremolite	+	+		+	+	+	+	+	+			+	+			+	+		
Augite		+	+	+	+		+	+											
Enstatite	+						+		+	+			+		+		+		+
Hypersthene	+		2	+		+	+	+		+		+			+			+	
Olivine		+		+		+	+	+		3		+			10.2	+		+	
Diopside		+	+		+		+	+	+			+				+	+	+	+

colour of the sediment. Higher percentages of coated grains were found in the reddish-brown sediments than in the greyish-brown material. The ore minerals include a wide variety of metallic grains including magnetite, ilmenite, and leucoxene. No significant distributional pattern was shown by any of these mineral groups. The translucent minerals are listed in Table I with the number frequency percentage of each. Most of the minerals in the varied, immature suite have been observed as accessory minerals in thin sections in the local sedimentary formations, and the sand appears to come from the local rock formations surrounding the sample area. The lack of variety in the distribution of the principal minerals indicates that the source area is too small and uniform to produce any distinct heavy mineral anomalies.

The colour of sandy and muddy samples was determined by comparison of the dried sample with the Munsell Soil Color Chart. The variation in colour found within the sample area is illustrated in Fig. 14. Greyish-brown was the most common colour. Sediments of this colour cover the whole of Kouchibouguac Bay and a 3–10-km wide strip outside the bay. East of this strip a progressive change from greyish-brown to red occurs. This change is shown by a series of colour belts, brown, reddish-brown, and red, that parallels the coast of Prince Edward Island. This variation in colour corresponds to the composition of the associated gravel and bedrock. The greyish-brown sandstone is probably derived from the grey Richibucto Formation whereas the source of the brown and reddish-brown rocks is the reddish-brown Scouduc formation and the red rocks of Prince Edward Island. The boundary between the reddish-brown sediments and the red material is distinct in the area of the deep trough off Prince Edward Island, and may mark the western limit of the sandstone of Prince Edward Island.

REFERENCES

BLACKFORD, B. L. 1965. Results from a Current Water moored in Kouchibouguac Bay, June and July, 1964. Fish. Res. Bd. Canada, MS Rept. Ser. (Oceanog. Limnol.). No. 196.

DUANE, D. B. 1964. Significance of skewness in recent sediments, western Pamlico Sound, North Carolina. J. Sediment. Petrol., **34**(4): 864–874.

FOLK, R. L., AND WARD, W. C. 1957. Brazos River bar: A study in the significance of grain size parameters. Ibid., **27**: 3–27.

FRIEDMAN, G. M. 1961. Distribution between dune, beach, and river sands from their textural characteristics. Ibid., **31**: 514–529.

1962. Sorting coefficients and the lognormality of the grain size distribution of sandstones. J. Geol., **70**: 737–753.

GOLDTWAIT, J. W. 1924. Physiography of Nova Scotia. Am. J. Sci., **241**: 117–123.

GUSSOW, W. C. 1953. Carboniferous stratigraphy and structural geology of New Brunswick, Canada. Am. Assoc. Petrol. Geol., **37**(7): 1713–1816.

HJULSTRÖM, F. 1939. Transportation of detritus by moving water. *In* P. D. Trask [ed.] Recent marine sediments. Am. Assoc. Petrol. Geol., Tulsa. p. 5–31.

INMAN, D. L. 1952. Measures for describing the size distribution of sediments. J. Sediment. Petrol., **22**(3): 125–145.

KRUMBEIN, W. C., AND PETTIJOHN, F. J. 1938. Manual of sedimentary petrology. Appleton-Century-Crofts, Inc, New York. 549 p.

LUNDQUIST, G. 1935. Block Undersokningar; Historik och Metodik. Sveriges Geol. Undersokn. Arsbok Ser. Ca. Avhandl. Uppsat., No. 21.

MARTIN, L. R. 1965. Significance of skewness and kurtosis in environmental interpretation. J. Sediment. Petrol., **35**(3): 768.

MASON, CURTIS C., AND FOLK, ROBERT L. 1958. Differentiation of beach, dune and aeolian flat environments by size analysis. Mustang Island, Texas. Ibid., **28**: 211–226.

PETTIJOHN, F. J. 1957. Sedimentary rocks. Harper and Brothers, New York. 718 p.

SHEPARD, F. P. 1963. Submarine geology. Harper and Row Publishers, New York, Evanston and London. 557 p.

SHEPARD, F. P., AND INMAN, D. L. 1950. Nearshore water circulation related to bottom topography and wave refraction. Trans. Am. Geophys. Union, **31**(2): 196–212.

WEEKS, L. J. 1963. The Appalachian region, in geology and economic minerals of Canada. Geol. Surv. Canada. Economic Geology Ser., No. 1, 4th ed.

Hematological Aspects of the Thermoacclimatory Process in the Rainbow Trout, *Salmo gairdneri*[1,2]

BY MARY ANNE DEWILDE AND A. H. HOUSTON

Department of Biology
Marquette University, Milwaukee, Wisconsin

ABSTRACT

The blood oxygen capacity of the rainbow trout has been investigated as a function of thermal acclimation in terms of erythrocyte abundance, packed cell volume, hemoglobin concentrations, and mean erythrocytic volume and hemoglobin content. Fish at the lower acclimation temperatures employed (3, 7 C) were characterized by relatively low erythrocyte counts, hematocrits, and hemoglobin levels. Mean erythrocyte volumes tended to be relatively high, whereas mean erythrocytic hemoglobin content was somewhat below that typical of the higher temperature groups. In general, animals held at intermediate temperatures (11, 14, 17 C) showed significant increases in oxygen-carrying capacity by comparison with cold-acclimated fish. Finally trout at 21 C typically had larger numbers of somewhat smaller red cells, more hemoglobin, and higher levels of hemoglobin per erythrocyte than either the low- or intermediate-temperature fish. Significant differences were observed between summer and fall–winter series of trout, particularly with respect to hemoglobin levels. The results are discussed in relation to the general problem of respiratory thermoadaptation.

INTRODUCTION

VARIATIONS IN environmental temperature impose a variety of stresses upon the teleost fish, not least of which are those associated with respiratory requirements. Oxygen consumption in relation to temperature can often be described for fishes in terms of a parabolic function in two constants having the general form, $\dot{V}_{O_2} = K_0 \cdot T^{K_1}$, or its arithmetic equivalent, $\dot{V}_{O_2} = K_0 + K_1 \cdot T$, i.e. the well-known Bělehrádek and Krogh metabolism–temperature curves. The second constant, K_1, which represents the Van't Hoff Q_{10} for overall oxidative metabolism, may have values ranging from about 2 to 10 depending upon the species and temperature zone under consideration (Winberg, 1956; Fry, 1957). The effect of temperature upon oxygen solubility, however, is such that the teleost exposed to elevated temperature conditions must satisfy a much-heightened oxygen demand in an environment which has become relatively hypoxic.

Despite the emphasis in recent years upon investigation of the thermal relationships of fishes, there has been surprisingly little attention directed toward the functional adaptations which permit solution of this problem. Several possible modes of response are, however, suggested by the recent theoretical and experimental studies of Hughes (1964), Rahn (1966), and

---

[1] Received for publication June 26, 1967.

[2] Supported by National Science Foundation Grant GB-4212, and the Marquette University Committee on Research.

J. FISH. RES. BD. CANADA, 24(11), 1967.
Printed in Canada.

Randall et al. (1967). In each instance respiratory exchange has been analyzed in terms of models, based upon the known operation of compact heat exchangers, which incorporate as primary variables ventilatory flow ($\dot{V}_G$), branchial blood flow ($\dot{V}_B$), exchange surface area (A), blood oxygen capacity ($\alpha\ B_{O_2}$), water oxygen solubility ($\alpha\ W_{O_2}$), inspiratory and expiratory water tensions ($P_{O_2,WI}$, $P_{O_2,WE}$), and venous and arterial blood oxygen tensions ($P_{O_2,BV}$, $P_{O_2,BA}$).

That attempts to compensate for an increase in oxygen requirement ($\dot{V}_{O_2}$) solely through increases in $\dot{V}_G$ may become rapidly self-limiting is suggested by a number of studies. Schuman and Piiper (1966), for example, have shown that the branchial pump consumes about 30% of the resting metabolism of the tench, *Tinca tinca*, and may account for as much as 70% at maximum ventilation rates. In addition, increases in flow velocity reduce the exposure time of any given volume of water to the exchange surface whereas increases in ventilatory stroke volume increase the diffusional deadspace. Furthermore, increases in $\dot{V}_G$ lead to the shunting of a substantial portion of the respiratory current between adjacent branchial arches rather than over the exchange surfaces (Pasztor and Kleerekoper, 1962). The net result is frequently a marked diminuition of the efficiency of oxygen extraction as maximum ventilatory flow rates are approached (Saunders, 1962; Randall et al., 1967). Thus, a good deal of the potential benefit of elevating V_G is undoubtedly dissipated as a consequence of the increased metabolic cost of operating the branchial pump and the reduced efficiency of the exchanger system.

Modification of $\dot{V}_B$ (essentially cardiac output in teleosts) presents another possible mode of compensation. $\dot{V}_B$ can be varied as a function of either heart rate or stroke volume; and although the energy demands of operating the cardiac pump have apparently not as yet been evaluated, they are presumably slight in relation to those of ventilation. However, Hughes' analysis of respiratory exchange (Hughes, 1964) suggests that variations in cardiac output, to be effective, must be closely coupled to changes in ventilation. Maximal blood oxygenation should be achieved as the capacity-rate ratio, $[\dot{V}_B \cdot \alpha\ B_{O_2} (P_{O_2,BA} - P_{O_2,BV})\ /\ \dot{V}_G \cdot \alpha\ W_{O_2} (P_{O_2,WI} - P_{O_2,WE})]$, approaches zero, since under such conditions $P_{O_2,BA}$ will approximate $P_{O_2,WI}$. Presumably, then, the degree to which $\dot{V}_B$ can be usefully increased will be limited by the extent to which it is metabolically practical to modify $\dot{V}_G$.

Hughes (1964) and Randall et al. (1967) have also related the effectiveness of blood oxygenation to exchange surface area, demonstrating that oxygen uptake should increase with increases in the branchial transfer unit parameter $A \cdot d/\dot{V}_B \cdot \alpha\ B_{O_2}$ where d = the coefficient of oxygen diffusion across the lamellar wall. Inasmuch as Steen and Kruyyse (1964) have identified alternate respiratory and non-respiratory flow patterns in the gill and the capacity of the teleost to shunt blood between these pathways, it seems possible that satisfaction of increased oxygen demand at higher temperatures might well be associated with some form of branchiovascular response which increases the functional value of A. However, a response of this sort is not without concomitant disadvantages. Transfer relationships comparable to those obtaining for oxygen must also exist for water, diffusible solutes, and carbon dioxide. Consequently, resort to this method of compensation might be expected to entrain increased endosmosis, electrolyte efflux, and reduced carbon dioxide tensions which, in turn, would require some adjustment in the water-electrolyte and acid-base regulating mechanisms.

Finally, satisfaction of increased oxygen demand could be achieved through an increase in the blood oxygen capacity factor, $\alpha\ B_{O_2}$. A response of this type, aside from the costs of erythrocyte elaboration and hemoglobin synthesis, would seem to impose no further major restrictions upon the system as a whole. Indeed, through provision of additional hemoglobin, an increase in buffer capacity might be anticipated, a factor of some importance in view of the increased metabolic activity associated with adaptation to higher temperatures. The total oxygen capacity of the blood represents the sum of the separate capacities of plasma and hemoglobin. Although the former might be expected to decline at elevated temperatures, an overall increase could be achieved by provision of additional hemoglobin. It should be pointed out, however, that hemoglobin oxygen capacity is not solely a function of the amount of hemoglobin available but depends upon the slope of the dissociation curve as well. Irving et al. (1941), working with the blood of *Salvelinus fontinalis*, have demonstrated a sharp right shift of the dissociation curve, accompanied by conversion from the hyperbolic to the sigmoid form with increases in temperature. Nevertheless, virtual saturation was obtained at temperatures less than 25 C. Similarly, Randall et al. (1967) report close to 100% effective oxygenation in resting rainbow trout at temperatures below 15 C. Consequently, it seems probable that under such conditions changes in $\alpha\ B_{O_2}$ can be estimated, without consideration of the dissociation curve, in terms of the more readily determined blood parameters.

The hematological correlates of the thermal acclimation process in teleosts have previously received some attention. The results obtained have, however, been notably inconsistent, even in studies upon the same species (e.g. Spoor, 1951; Anthony 1961a; Falkner and Houston, 1966). To provide further information pertinent to this aspect of the general phenomenon, an investigation of temperature-related variations in the hematology of the rainbow trout was undertaken as a component of a broader study of the thermoacclimatory process in freshwater teleosts. The basic protocol of the investigation involved acclimation of summer and fall–winter test groups of a single stock of animals to a series of temperatures spanning the near-high to near-low incipient lethal range of this species (i.e. approximately 0 to 24 C; Black, 1953). After acclimation the animals were killed; cardiac blood samples were taken; and determinations of erythrocyte number, packed cell volume, and total blood hemoglobin concentration were carried out. From these data, values for mean erythrocytic volume and hemoglobin content were estimated.

MATERIALS AND METHODS

EXPERIMENTAL STOCK

The animals used in the investigation represented a single yearling stock of trout, and were reared at the Nevin Hatchery of the Wisconsin State Conservation Department. After transportation to the laboratory, the fish were maintained in 250-gal, self-flushing, fiber-glass tanks housed in a walk-in freezer room, and supplied from dechlorinating columns. Tank temperatures were regulated by means of thermistor-activated relays governing the operation of resistance heaters. The latter were wrapped with plastic tape to minimize ionic contamination of the water. Water temperatures were continuously monitored in each tank, and ranged between ±0.2 C of set-point. Oxygen levels in the input water supply varied between 7.5 and 13.0 ppm during the period of acclimation. However, in the acclimation tanks, which were continuously aerated, oxygen concentrations were close to, or somewhat in excess of saturation at all times. By reference to values summarized by Fry (1957) for a related species, the brook trout, oxygen tensions were in excess of limiting values, and well above the concentrations prompting hematological response in the goldfish (Prosser et al., 1957). Weekly testing indicated the absence of free chlorine from the input water. *p*H values fluctuated between 7.2 and 7.8, being generally around 7.4.

The difficulties associated with the establishment of similar nutritional states among groups of poikilotherms held at different temperatures have been commented upon by Prosser (1962). In the immediate context of the present study, Kamra (1966) has shown that extreme variations in the nutritional levels of Atlantic cod are associated with significant changes in some hematological parameters, notably packed cell volumes. In the present investigation, all groups were fed once daily, ad libitum, in the early morning upon a pelletted ration provided by the parent hatchery. Under this regime they remained in active and apparently healthy condition. However, there can be little doubt that the various acclimation groups did differ in nutritional status, and the effect of this has yet to be ascertained.

After arrival at the University, all animals were held at 8–10 C for at least 2 weeks. Thereafter, tank temperatures were changed approximately 1 C per day until the desired acclimation temperature was reached. Details pertinent to acclimation temperatures and durations, sample sizes and body weights, and sampling dates are recorded in Table I for the summer and fall–winter series of fish used.

SAMPLING

Individual animals were anesthetized before sampling in aqueous tricaine methane sulphonate (M.S. 222, Sandoz), the concentration of which was adjusted as required to produce narcosis in 3–4 min. In the case of the smaller animals used in the summer series, it was found most convenient to draw blood samples directly from the exposed heart. For larger specimens, however,

TABLE I.

Acclimation temp (*C*)	Sample size		Sample weights		Sampling dates	
	Summer	Fall–winter	Summer	Fall–winter	Summer	Fall–winter
3	13	15	29.2 ± 4.9(21.9–38.9)[a]	112.7 ± 9.5(96.6–127.4)	July 26, 27 (1966)	Jan. 19 (1967)
7	12	15	28.5 ± 5.8(18.9–42.9)	125.5 ± 32.0(44.0–170.5)	July 19–21 (1966)	Dec. 19 (1966)
11	12	10	27.7 ± 4.3(22.2–37.4)	68.9 ± 10.2(54.6–94.4)	July 5–8 (1966)	Sept. 25 (1966)
14	15	20	30.7 ± 3.9(20.0–37.3)	104.5 ± 10.0(86.3–117.9)	July 11, 12 (1966)	Oct. 22–26 (1966)
17	22	10	32.3 ± 5.5(23.7–41.7)	80.3 ± 10.9(65.2–99.3)	July 14–19 (1966)	Sept. 16 (1966)
18	–	20	–	135.8 ± 19.3(95.7–180.7)	–	Jan. 9–18 (1967)
21	15	10	31.5 ± 5.8(25.7–46.6)	83.3 ± 21.5(57.8–73.1)	July 22–26 (1966)	Sept. 1 (1966)

[a] Mean + standard deviation (range).

this approach provided no advantage over the direct cardiac puncture technique. Heparin, recommended by Hesser (1960) and Anthony (1961a) was found to be unsatisfactory in fully preventing coagulation of rainbow trout blood. However, in combination with ethylenediaminetetraacetate (EDTA), the ammonium salt proved adequate for the purposes of the study.

HEMATOLOGICAL METHODS

Erythrocyte counts were carried out in quadruplicate according to the procedure suggested by Hesser (1960), using Hendricks' fluid as a diluting medium (Hendricks, 1952). Duplicate microhematocrit estimates were made upon samples drawn into 1.5 × 75-mm tubes, sealed with Seal-Ease (Clay-Adams), and centrifuged at 15,000 r.p.m. for 4 min. No corrections for trapped plasma were applied. All samples in which the plasma showed visible signs of hemolysis or in which cell clumping was observed during erythrocyte enumeration were discarded.

Estimates of blood oxygen capacity in teleosts have been largely based upon methods developed for use in the determination of mammalian hemoglobin levels. Some controversy surrounds the validity of their use with fish blood, and this has led to several methodological studies in recent years (e.g. Hesser, 1960; Larsen and Snieszko, 1961; Anthony, 1961a). Despite its well-established deficiencies (Henry, 1964), the acid-hematin technique has been extensively used in hematological studies upon salmonids (e.g., Black et al., 1960; Schiffman and Fromm, 1959). Larsen and Sniezsko (1961) have compared the acid-hematin, oxyhemoglobin, and cyanmethemoglobin methods for the determination of hemoglobin levels in trout, using total blood iron as a reference standard. In a more extensive survey, Anthony (1961a) used the Van Slyke CO method for provision of reference values and compared the total blood iron method, and the alkaline hematin, cyanhematin, carboxyhemoglobin, oxyhemoglobin, and pyridine hemochromogen derivatives of hemoglobin as measures of oxygen capacity in goldfish blood. These studies, with those of Hesser (1960), clearly indicate the inadequacy of methods based upon hematin derivatives. It is also apparent that standardization of the Haldane and oxyhemoglobin procedures presents several problems.

On the basis of these studies, the pyridine hemochromogen method was selected for use in the present investigation. This method measures most of the normally occurring forms of hemoglobin (Henry, 1964) including methemalbumin derivatives (Fleisch, 1960), a factor felt to be of some importance in view of the marked fragility of teleost erythrocytes (Lewis and Ferguson, 1966). However, the determination also includes several inactive derivatives of hemoglobin (e.g. sulfhemoglobin) as well as the oxygen carriers. Accordingly, the values reported are probably somewhat higher than the actual functional concentrations.

The procedure followed was essentially that described by Anthony (1961a). Twenty rather than 25-μl samples of blood were used, and optical densities were read at 560 mμ (Henry, 1964). Freshly prepared dilutions of Hemotrol

(Clinton Laboratories) were employed as bracketting standards for each series of determinations. This standard, a stabilized human whole blood hemoglobin, is itself standardized at source by the total iron, oxyhemoglobin, and cyanmethemoglobin methods.

Values for erythrocyte numbers ($10^6/\text{mm}^3$), packed cell volume (%) and hemoglobin (g/100 ml whole blood) were used to estimate mean erythrocytic volume and hemoglobin content using the following relationships:

$$\text{Mean erythrocytic volume} = (\text{packed cell volume}/\text{erythrocyte numbers}) \cdot (10),\ \mu\text{l}$$
$$\text{Mean erythrocytic hemoglobin} = (\text{hemoglobin} \times 100/\text{packed cell volume}),\ \%.$$

DATA ANALYSIS

Statistical analysis of the data was carried out by the University Computing Center under the supervision of Mr Brian Walsh. For each acclimation group, values for the mean, range, standard deviation, and standard error of each variant measured (weight, fork length, erythrocyte count, packed cell volume, total blood hemoglobin, and mean erythrocytic volume and hemoglobin content) were calculated. Correlation coefficients relating each variant to all other variants were provided by the program employed as was an evaluation of the frequency distribution of the data. Group variant comparisons were based upon application of Student's *t*-test. Summer and fall–winter series of fish were compared at each temperature used, whereas the values obtained within each series were compared for all temperature combinations. Assignment of significance values was based upon the *r*- and *t*-tables provided by Snedecor (1953).

RESULTS

Data obtained in the study are summarized in Fig. 1 and 2, and Table II.

Group-by-group and lumped frequency distribution analyses of the parameters investigated indicated a sufficiently close approximation to normality to justify employment of the statistics used in this study. A similar group-by-group correlation study revealed no consistently significant ($P > 0.05$) variation of any parameter with either weight or fork length. It may be noted, however, that erythrocyte levels usually varied inversely with weight ($r = -0.058$ to -0.425) and fork length ($r = -0.126$ to -0.401), suggesting an age-related variation in their abundance.

ERYTHROCYTES

Although the summer and fall–winter samples of fish differed significantly ($P > 0.05$) at two acclimation temperatures (7, 17 C), a similar trend toward an increase in erythrocyte number at higher temperatures was observed in each instance. The results of *t*-test analyses carried out for all combinations of groups (Table II) indicated that the erythrocyte levels of the 3 and 7 C trout of both summer (1.09 ± 0.02; $1.14 \pm 0.04 \times 10^6/\text{mm}^3$) and fall–winter series (1.19 ± 0.04; $1.25 \pm 0.03 \times 10^6/\text{mm}^3$) were significantly lower than those of animals acclimated to all higher temperatures ($P > 0.05$ to 0.001).

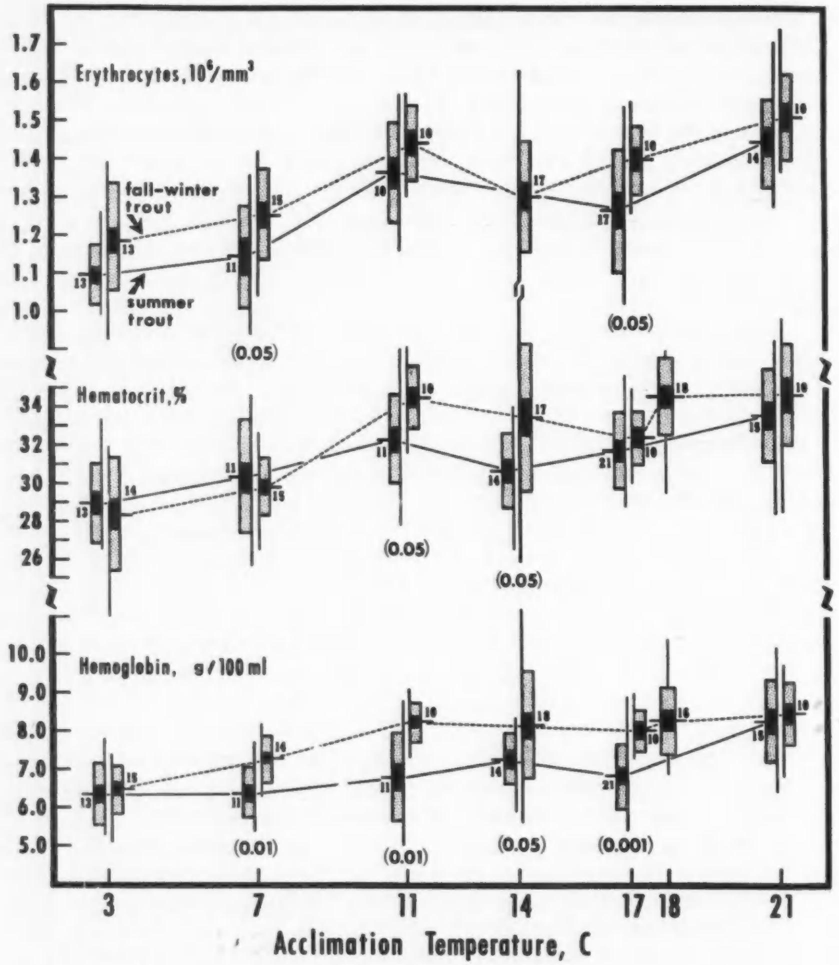


FIG. 1. Erythrocyte, hematocrit, and hemoglobin levels in summer and fall–winter series of rainbow trout as a function of acclimation temperature: horizontal line: sample mean; vertical line: sample range; solid vertical bar: standard error; open vertical bar: standard deviation; small numerals: sample size; bracketted numerals: level of significance of difference between summer and fall–winter series of fish.

Similarly, the red cell numbers of the 21 C fish of both summer ($1.44 \pm 0.08 \times 10^6/\text{mm}^3$) and fall–winter series ($1.51 \pm 0.04 \times 10^6/\text{mm}^3$) were significantly higher than those of animals at all lower test temperatures ($P > 0.05$ to 0.001) except 11 C. By contrast, fishes at 11, 14, and 17 C tended to have rather similar erythrocyte numbers. Thus, the general form of the relationship be-

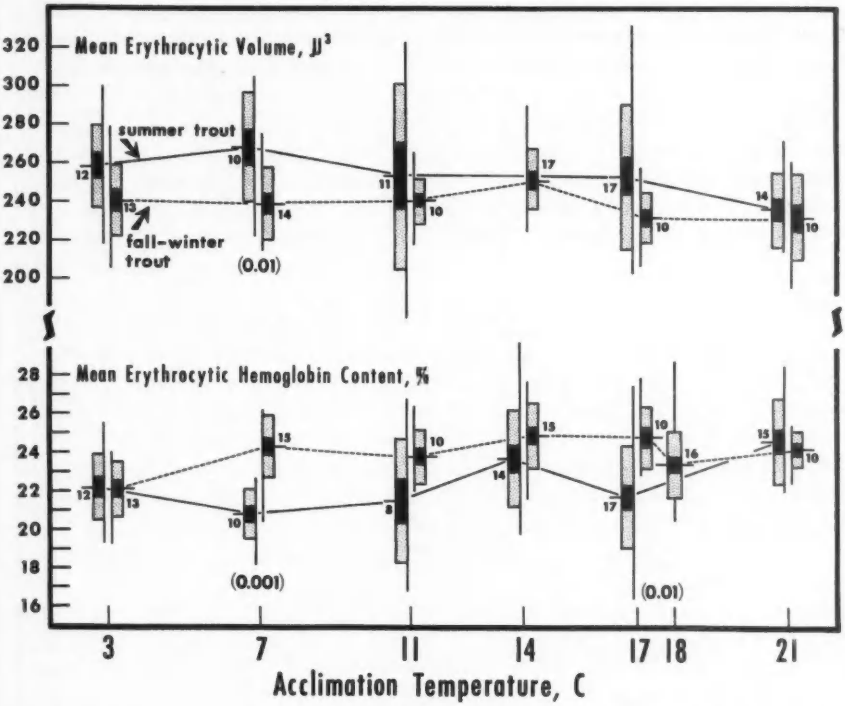


FIG. 2. Mean erythrocyte volume and hemoglobin content in summer and fall–winter series of rainbow trout as a function of acclimation temperature: horizontal line: sample mean; vertical line: sample range; solid vertical bar: standard error; open vertical bar: standard deviation; small numerals: sample size; bracketted numerals: level of significance of difference between summer and fall–winter series of fish.

tween red cell abundance and acclimation temperature is that of a generally ascending curve with some suggestion of an intermediate plateau.

PACKED CELL VOLUME

As might be anticipated, much the same sort of relationship obtained for packed cell volume. Summer and fall–winter trout showed significant differences ($P > 0.05$) at two test temperatures (11, 14 C) although the general form of the relationship was similar in both series. Among the summer animals, the hematocrit level (29.0 ± 0.6%) was significantly lower ($P > 0.1$ to 0.01) in fish acclimated to 3 C than in those maintained at 11, 17, and 21 C (31.7 ± 0.4% to 33.6 ± 0.6%). It was not, however, significantly different from that typical of 7 C fish (30.3 ± 0.9%). With one exception (the 11 C acclimation group), animals at 21 C were characterized by significantly higher hematocrits than were characteristic of trout held at all lower temperatures. The fall–

TABLE II. *t*–Test analysis.

		Summer series (*C*)					Fall–winter series (*C*)					
Parameter	Temp (*C*)	7	11	14	17	21	7	11	14	17	18	21
RBC	3	NS	.001	–	.01	.001	NS	.001	0.5	.001	–	.001
	7	–	.01	–	.05	.001	–	.001	NS	.01	–	.001
	11	–	–	–	NS	NS	–		.02	NS	–	NS
	14	–	–	–	–	–	–	–	–	NS	–	.001
	17	–	–	–	–	.01	–	–	–	–	–	.05
PVC	3	NS	.01	NS	.01	.001	NS	.001	.001	.001	.001	.001
	7	–	NS	NS	NS	.01	–	.001	.01	.001	.01	.001
	11	–	–	NS	NS	NS	–	–	NS	.01	NS	NS
	14	–	–	–	NS	.01	–	–	–	NS	NS	NS
	17	–	–	–	–	.05	–	–	–	–	.01	.05
	18	–	–	–	–	–	–	–	–	–	–	NS
Hb	3	NS	NS	NS	NS	.001	.01	.001	.001	.001	.001	.001
	7	–	NS	.01	NS	.01	–	.001	.05	.01	.01	.001
	11	–	–	NS	NS	.01	–	–	NS	NS	NS	NS
	14	–	–	–	NS	.01	–	–	–	NS	NS	NS
	17	–	–	–	–	.001	–	–	–	–	NS	NS
	18	–	–	–	–	–	–	–	–	–	–	NS
MEV	3	NS	NS	–	NS	.05	NS	NS	NS	NS	–	NS
	7	–	NS	–	NS	.01	–	NS	NS	NS	–	NS
	11	–	–	–	NS	NS	–	–	NS	NS	–	NS
	14	–	–	–	–	–	–	–	–	.01	–	.05
	17	–	–	–	–	NS	–	–	–	–	–	NS
MEHbC	3	NS	NS	NS	NS	.01	.001	.01	.001	.001	.05	.01
	7	–	NS	.01	NS	.001	–	NS	NS	NS	NS	NS
	11	–	–	NS	NS	.02	–	–	NS	NS	NS	NS
	14	–	–	–	.05	NS	–	–	–	NS	.05	NS
	17	–	–	–	–	.01	–	–	–	–	NS	NS
	18	–	–	–	–	–	–	–	–	–	–	NS

winter series of trout resembled the summer animals in that both low temperature groups differed significantly from the 11 through 21 C animals. Consequently, the overall relationship bears a strong resemblance to that for erythrocyte abundance.

HEMOGLOBIN

Differences in hemoglobin concentrations significant at the 0.05–0.001 levels were found between summer and fall–winter animals at all intermediate temperatures (7 to 17 C). With the exception of the 7 versus 14 C animals, comparisons of all groups of summer fish between 3 and 17 C failed to show significant differences. By contrast, the hemoglobin level at 21 C (8.3 ± 0.3

g/100 ml) was significantly higher than that of all lower temperature groups (6.4 ± 0.2 to 7.3 ± 0.2 g/100 ml).

Of the fall–winter series, the 3 C animals had a lower hemoglobin level (6.4 ± 0.2 g/100 ml) than all groups from 7 to 21 C. Similarly, the mean hemoglobin concentration of fish at 7 C (7.3 ± 0.2 g/100 ml), although higher than that at 3 C, was significantly lower than those observed at higher temperatures. No significant differences existed between the 11, 14, 17, 18, and 21 C animals. Accordingly, the general relationship between hemoglobin and temperature in this series of animals tends to resemble that seen for erythrocyte numbers and packed cell volumes.

Mean Erythrocytic Volume

Erythrocytic volumes for summer and fall–winter trout differed significantly at only one test temperature, 7 C. Furthermore, *t*-test values for the summer fish were significant for only two temperature combinations; 3 versus 21 C ($P > 0.05$) and 7 C versus 21 C ($P > 0.01$). Much the same sort of situation obtained for the fall–winter series. Significant variations were encountered only between the 14 versus 17 C ($P > 0.01$), and 14 versus 21 C ($P > 0.05$) groups. Thus, the variables employed in the study do not appear to influence mean erythrocytic volume greatly.

Mean Erythrocytic Hemoglobin Content

The situation for mean erythrocytic hemoglobin values appeared to be intermediate in type by comparison with the other hematological parameters observed. Significant differences between the two series of trout used were seen at 7 ($P > 0.001$) and 17 C ($P > 0.01$). Among the fall–winter animals, those at 3 C had lower mean erythrocytic hemoglobin levels than were characteristic of all higher acclimation groups ($P > 0.05$–0.001). With one exception (14 versus 18 C; $P > 0.05$), no other significant variations were seen. A more diversified picture was typical of the summer series of fish. The low-temperature animals were, like the corresponding fall–winter trout, characterized by a mean erythrocytic hemoglobin level (22.2 ± 0.5%) lower than that of 21 C fish (24.6 ± 0.6%), but not greatly different from those typical of the 7–17 C groups (20.8 ± 0.4 to 23.7 ± 0.7%). That typical of 7 C trout (20.8 ± 0.4%) was significantly less than those of 14 (23.7 ± 0.7%) and 21 C (24.6 ± 0.6%) fish. Trout held at 11, 14, and 17 C each differed from one additional group (11 versus 21 C; 14 versus 17 C; 17 versus 21 C).

In general, the data support the hypothesis that some hematological modification accompanies thermal acclimation in this species. By comparison with other test groups, trout maintained at the lowest temperatures used had fewer, but possibly somewhat larger erythrocytes, considerably less total hemoglobin, and possibly less hemoglobin per cell. Little evidence of any consistent variation was apparent at intermediate temperatures. At the highest temperatures, however, the picture was, on the whole, one of an increase in erythrocyte number, a possible reduction in cell size, and, by comparison with low temperature trout, a marked increase in total hemoglobin. The latter variation seemed also to be reflected in a slight increase in the amount of hemoglobin per erythrocyte.

DISCUSSION

The values obtained in this study are generally comparable to those reported in earlier investigations upon the hematology of this species (e.g. Schiffman and Fromm, 1959; Black et al., 1960, 1962; Black and Connor, 1964). The most notable differences are seen with respect to hemoglobin concentrations. Those reported by Schiffman and Fromm (1959) are well below the values typical of animals held under essentially similar temperature conditions in this study. By contrast, the hemoglobin levels observed by Black and his co-workers, although more variable, are generally higher. It seems probable that the discrepancies are in large measure attributable to differences in the analytical procedures used. Schiffman and Fromm (1959) employed the acid-hematin technique, centrifuging to avoid the turbidity arising from suspended cell nuclei. Larsen and Snieszko (1961) found this procedure to yield values some 25–35% lower than those calculated from total blood iron concentrations. Use of the unmodified acid-hematin procedure, the technique generally followed by Black, was associated with hemoglobin levels which were approximately 40% higher than those estimated from blood iron values.

No earlier studies upon thermoadaptive modifications in the hematology of salmonid species are known to the authors. Investigations upon other teleosts, however, present a most varied picture. For example, whereas Spoor (1951) reported a positive correlation between erythrocyte numbers and acclimation temperature in goldfish, Falkner and Houston (1966) found no significant differences between animals held at 20 and 30 C; and Anthony (1961a) reported an inverse relationship between red blood cell count and temperature in the same species. Much the same sort of situation also obtains with respect to reported values for packed cell volumes. Both trout and goldfish do, however, tend to show variations in mean erythrocytic volume with temperature. Changes in cell volume were also reported by Irving et al. (1941) who attributed them to modifications in pCO_2, an hypothesis consistent with modifications in water-electrolyte and acid-base regulation during thermal acclimation (Heinicke and Houston, 1965; A. H. Houston et al., unpublished data). Anthony (1961a) reported some increase in the oxygen-carrying capacity of individual red cells at higher temperatures. This was not observed by Falkner and Houston (1966) although changes in the relative abundance of some hemoglobin polymorphs were reported. With respect to the rainbow trout, the mean erythrocytic hemoglobin content was significantly higher at 21 C than at 3 C in both summer and fall–winter animals.

On the whole, the data obtained in the present study do not indicate that modifications in blood oxygen capacity are of major importance in the solution of the temperature–oxygen demand problem. The situation contrasts strongly, therefore, with the marked hematological changes associated with acclimation by teleosts to hypoxic conditions (Prosser et al., 1957).

On the other hand, there is some support for the suggestion that the hematological responses which do occur take place in approximately stepwise fashion. The observation that cold-acclimated animals are characterized by relatively few erythrocytes, and low total and mean erythrocytic hemoglobin values was not unexpected. Anthony (1961b) has shown that the goldfish can survive indefinitely at low temperatures (5 C) with virtually complete carbon monoxide blockage of the oxygen transport system. Presumably under cold conditions, with $\dot{V}_{O_2}$ at a minimum and with αW_{O_2} and the plasma oxygen capacity close to their maxima, there is little stimulus for either red cell elaboration or hemoglobin synthesis. The generally low levels observed may well reflect uncompensated cell death, and might have been further lowered by a more prolonged acclimation to the temperatures used. It is perhaps noteworthy in this context that cold-acclimated goldfish display relatively high levels of plasma proteins whose mobilities and staining properties suggest an equivalency to the mammalian haptoglobin group (J. C. Fenwick and A. H. Houston, unpublished data).

Exposure to higher temperatures (7 to 11 C) does, however, appear to prompt an increase in red cell numbers; and in winter trout at least, this is associated with a significant rise in the hemoglobin level. Between this temperature range and 17 C, no further consistently significant changes were apparent. This constitutes, perhaps, the most surprising feature of the data since, over this intermediate zone of temperatures, $\dot{V}_{O_2}$ for rainbow trout rises by approximately 100% (Flörke et al., 1954; Evans et al., 1962). Consequently we are led to conclude that, in the rainbow trout as in the goldfish (Falkner and Houston, 1966), all, or some combination of the other functional variables (i.e. $\dot{V}_G$, $\dot{V}_B$, A) are adjusted to permit satisfaction of respiratory requirements.

A second increase in oxygen capacity appears to accompany acclimation of the animals to 21 C, a temperature close to their upper incipient lethal level. Again this was particularly noticeable among animals of the summer series, but also apparent in fall–winter trout as well. By comparison with all values for trout maintained between 11 and 17 C, the hemoglobin and erythrocyte levels of the 21 C animals rose by as much as 20 to 25%. Inspection of the data reported by Flörke et al. (1954) for oxygen consumption in rainbow trout suggests that $\dot{V}_{O_2}$ also increases by approximately the same amount with this further elevation in acclimation temperature. Accordingly, it is tempting to speculate that whereas variations in $\dot{V}_G$, $\dot{V}_B$, and A may suffice to meet oxygen demand within the intermediate temperature zone, they are no longer feasible, for the reasons alluded to earlier, as the upper temperature extreme is approached. At this point a further increase in αB_{O_2} may be invoked to meet the additional demand imposed by higher temperatures. It should, however, be noted that an alternate hypothesis is suggested by the work of Irving et al. (1941) upon the oxygen dissociation curve of trout blood. Data relating P_{O_2} tension for half-saturation of hemoglobin at physiological levels of P_{CO_2} against temperature appear to be discontinuous, inflecting between 15 and 20 C. Consequently, there appears to be some basis for the suggestion that at higher temperatures oxygen loading is inhibited, and that this might be compensated for by provision of additional capacity. Investigations related to both aspects of the general problem have recently been initiated in this laboratory and will be reported upon at a later date.

ACKNOWLEDGMENTS

The financial support of the National Science Foundation and the Marquette University Committee on Research is gratefully acknowledged, as is the generosity of the Wisconsin State Conservation Department in providing the stocks of trout used. Mr Brian Walsh of the University Computing Center gave unstinting assistance in the statistical analysis of the data.

REFERENCES

Anthony, E. H. 1961a. The oxygen capacity of goldfish (*Carassius auratus* L.) blood in relation to thermal environment. J. Exptl. Biol., **38**: 93–107.

1961b. Survival of goldfish in presence of carbon monoxide. Ibid., **38**: 109–125.

Black, E. C. 1953. Upper lethal temperatures of some British Columbia freshwater fishes. J. Fish. Res. Bd. Canada, **10**: 196–210.

Black, E. C., and A. R. Connor. 1964. Effects of MS 222 on glycogen and lactate levels in rainbow trout (*Salmo gairdneri*). Ibid., **21**: 1539–1542.

Black, E. C., A. R. Connor, K. C. Lane, and W. G. Chiu. 1962. Changes in glycogen, pyruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. Ibid., **19**: 409–436.

Black, E. C., A. C. Robertson, A. R. Hanslip, and W. G. Chiu. 1960. Alterations in glycogen, glucose and lactate in rainbow and Kamloops trout, *Salmo gairdneri*, following muscular activity. Ibid., **17**: 487–500.

Evans, R. C., F. C. Purdie, and C. P. Hickman. 1962. The effect of temperature and photoperiod on the respiratory metabolism of rainbow trout (*Salmo gairdneri*). Canadian J. Zool., **40**: 107–118.

Falkner, N. W., and A. H. Houston. 1966. Some haematogical responses to sublethal temperature shock in the goldfish, *Carassius auratus* L. J. Fish. Res. Bd. Canada, **23**: 1109–1120.

Fleisch, H. 1960. Mesure de l'hemolyse par la détermination dans le plasma de l'hémoglobine, la méthémalbumine et leurs dérivés. Helv. Med. Acta, **27**: 383–407.

Flörke, M., G. Keiz, and G. Wangerosch. 1954. Über die Temperature-Stoffwechsel-Relation und die Wärmeresistenz einiger Süswasser-Fische und des Flusskrebses. Z. Fischerei, **3**: 241–310.

Fry, F. E. J. 1957. The aquatic respiration of fish. *In* M. E. Brown [ed.] The physiology of fishes. Vol. 1. Academic Press, Inc., New York. p. 1–63.

Heinicke, E. A., and A. H. Houston. 1965. Some effects of sublethal thermal shock in the goldfish, *Carassius auratus*. J. Fish. Res. Bd. Canada, **22**: 1455–1476.

Hendricks, L. J. 1952. Erythrocyte counts and haemoglobin determinations for two species of sucker, genus *Catostomus*, from Colorado. Copeia, **4**: 265–266.

Henry, R. J. 1964. Clinical chemistry: principles and technics. Harper and Row. Evanston, Ill.

Hesser, E. F. 1960. Methods for routine fish haematology. Progressive Fish-Culturist, October: 164–170.

HUGHES, G. M. 1964. Fish respiratory homeostasis. *In* G. M. Hughes [ed.] Homeostasis and feedback mechanisms. Symp. No. 28. Soc. Exptl. Biol. p. 81–107.

IRVING, L., E. C. BLACK, AND V. SAFFORD. 1941. The influence of temperature upon the combination of oxygen with the blood of trout. Biol. Bull., **80**: 1–17.

KAMRA, S. K. 1966. Effect of starvation and refeeding on some liver and blood constituents of Atlantic cod (*Gadus morhua* L.). J. Fish. Res. Bd. Canada, **23**: 975–982.

LARSEN, N. H., AND S. F. SNIESKO. 1961. Comparison of various methods of determination of haemoglobin in trout blood. Progressive Fish-Culturist, **23**: 8–17.

LEWIS, J. H., AND E. E. FERGUSON. 1966. Osmotic fragility of pre-mammalian erythrocytes. Comp. Biochem. Physiol., **18**: 589–595.

PASZTOR, V. M., AND H. KLEEREKOPER. 1962. The role of the gill filament musculature in teleosts. Canadian J. Zool., **40**: 785–802.

PROSSER, C. L. 1962. Acclimation of poikilothermic vertebrates to low temperatures. *In* J. P. Hannon and E. Viereck [ed.] Comparative physiology of temperature regulation. Symp. No. 2, Arctic Aeromedical Laboratory, Ft. Wainwright, Alaska. p. 1–34.

PROSSER, C. L., L. M. BARR, R. D. PINC, AND C. Y. LAUER. 1957. Acclimation of goldfish to low concentrations of oxygen. Physiol. Zool., **30**: 137–141.

RAHN, H. 1966. Aquatic gas exchange: theory. Resp. Physiol., **1**: 1–12.

RANDALL, D. J., G. F. HOLETON, AND E. D. STEVENS. 1967. The exchange of oxygen and carbon dioxide across the gills of rainbow trout. J. Exptl. Biol., **46**: 339–348.

SAUNDERS, R. L. 1962. The irrigation of the gills in fishes. II. Efficiency of oxygen uptake in relation to respiratory flow activity and concentrations of oxygen and carbon dioxide. Canadian J. Zool., **40**: 817–862.

SCHIFFMAN, R. H., AND P. O. FROMM. 1959. Measurement of some physiological parameters in rainbow trout (*Salmo gairdneri*). Ibid., **37**: 25–32.

SCHUMAN, D., AND J. PIIPER. 1966. Der Sauerstoffbedarf der Atmung bei Fischen nach Messunger an der Narkotisierten Schleie (*Tinca tinca*). Pflug. Arch. Ges. Physiol., **288**: 15–26.

SNEDECOR, G. W. 1953. Statistical methods applied to experiments in agriculture and biology. Iowa State College Press.

SPOOR, W. A. 1951. Temperature and the erythrocyte count of goldfish. Federation Proc., **10**: 131.

STEEN, J. B., AND A. KRUYYSE. 1964. The respiratory function of teleostean gills. Comp. Biochem. Physiol., **12**: 127–142.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fishes. Fish. Res. Bd. Canada, Trans. Ser. No. 194. p. 1–202 (1960).

Temporal and Spatial Differences in Phytoplankton Productivity in Marion Lake, British Columbia[1]

By Ian E. Efford

Department of Zoology
University of British Columbia, Vancouver, B.C.

ABSTRACT

As shown by the C^{14} method, the primary productivity of phytoplankton in Marion Lake, a small shallow coastal lake, was very low and was concentrated almost entirely in the 5-month period June to October. Even on the sunniest days, productivity of the surface was not inhibited in contrast to results from most freshwater and marine studies. No explanation could be given. Measurements made simultaneously at 0.5 m at 20 stations covering the lake showed a trend to lower productivity as the water flowed from the inlet to the outlet except when the water passed a large spring. Here productivity increased, suggesting that nutrients were definitely limiting productivity. There was a close relationship between productivity and temperature but not between productivity and light. This suggested that the water temperature prevents full utilization of the available light energy and nutrients during 7 months of the year. The average producivity under a square metre of lake surface was estimated as only 8 g C/m² per year, and efficiency of conversion of available sun's energy to plant material as only 0.0009%. The low efficiency reflected the very low concentrations of nutrients in the lake water, the high flushing rate, and the low water temperature during 7 months of the year.

INTRODUCTION

The primary productivity of the phytoplankton in Marion lake was measured so that its role in providing energy to the lake system could be compared with the results of other studies on the productivity of the macrophytes in the lake and the energy entering the lake as detritus in the inflow water. The observations were designed to show the seasonal and spatial differences in the rate of energy fixation.

The study is part of a detailed analysis of the rate of energy flow and the related changes in species diversity in a small lake. The interest, therefore, centres around food production for the next trophic level. The C^{14} method was used because of the very low productivity in the lake and because it measures the increase in particulate carbon rather than photosynthesis. The method is ideal for measuring food production, as particulate carbon, because it does not measure material fixed during photosynthesis and later secreted from the cells (Watt, 1966; Nalewajko, 1966).

THE LAKE AND THE WATERSHED

Marion Lake, sometimes known as Jacob's Lake, is situated in southwestern British Columbia on the southern slopes of the large block of rugged

---

[1] Received for publication March 20, 1967.

J. Fish. Res. Bd. Canada, 24(11), 1967.
Printed in Canada.

Coast Mountains, which rise abruptly to 2000 m from the northern edge of the Fraser Valley. It is 50 km east of Vancouver and 10 km north-northeast of the village of Haney (49°19′N, 122°33′W). The granitic Coast Mountains have arisen since the early Jurassic and have been repeatedly uplifted. The resistant cores of granitic and metamorphic rocks now stand high above the adjacent areas; in the immediate vicinity of the lake the highest of these peaks is Mt. Blanchard, rising to 1707 m just 6.5 km to the northeast of the lake (Armstrong, 1957).

In the southwest corner of this block of the Coast Mountains the valleys are U-shaped in cross section and have irregular, north–south oriented longitudinal profiles. Marion Lake is itself situated in one such valley which lies at 300 m above sea level in the hills between two much deeper valleys, that of Pitt Lake to the west and Alouette Lake to the east.

The region was glaciated repeatedly during the Pleistocene (Armstrong, 1957) and at times the overriding ice sheets reached a thickness of 2300 m near the coast and even greater thickness inland. The ice sheet probably covered the region of the lake as recently as 11,500 B. P. After the disappearance of the ice the land surface rose so that some marine deposits and deltas in the region are up to 175 m above the present sea level in parts of the Coast Mountains. There is no evidence, however, that during the most recent glaciation the land was depressed to such an extent that the Marion Lake area was itself under the sea. Armstrong (1957) does indicate that this may have been possible during the Vachon Glaciation, which is thought to have lowered the land surface at least 300 m. If the area was inundated at that time no marine deposit now remains in or around the present-day lake.

The valley in which the lake is situated is narrow (500 m) and not very deep (300 m). The floor is covered with glacial drift and the hills on each side of the valley are either hornblende granitic rocks of quartz diorite or they are highly metamorphised hornblendic Upper Palaeozoic or Lower Mesozoic rocks (Roddick and Armstrong, 1956).

The southern part of the Coast Mountains lies within the littoral climatic region (Kendrew and Kerr, 1955) but, because of the mountains themselves, the mild humid winters characteristic of this climatic region are modified in having very heavy rainfall and sometimes heavy snow. Marion Lake has an average annual rainfall of 240 cm (94 inches) (Table I) and the lowest mean monthly temperature is only 2.9 C. The climate can be described as mild and wet. Kendrew and Kerr (1955) state that in the littoral climatic region there is a "pronounced dry season with bright sunny days" in July and August. This is not usually the case at the altitude of Marion Lake as these months sometimes have a considerable number of days with rain (Table I). There were only 118 rain-free days in the year ending July 1, 1964 and considerably fewer cloud-free days (Canada, Department of Transport, 1963 and 1964).

The southern part of the Coast Mountains below an altitude of approximately 600 m is in the dry subzone of the Coastal Western Hemlock zone

Table 1. Average monthly temperatures and rainfall at the University Forestry Reserve meteorological station 1 mile south of Marion Lake, 1954–64.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Rainfall (*cm*)	28.9	25.7	20.6	16.7	11.2	12.2	6.7	10.4	14.5	25.5	32.7	34.4	239.5
Days with rain July 63–July 64	30	20	24	24	18	21	14	14	12	24	26	24	
Temperature (C)	1.7	3.8	4.3	7.6	11.6	13.7	16.2	15.9	13.6	9.4	4.7	2.9	

(Orloci, MS, 1964). Logging and reforestation, however, have resulted in the drainage area being covered largely by recent secondary growth of the western hemlock (*Tsuga heterophylla*) and the western red cedar (*Thuja plicata*) except in the delta of the inlet stream.

Marion Lake was formed either in a depression in the glacial drift left as the ice retreated up the valley or from the damming of the valley by a small terminal moraine left by the retreating ice. Preliminary pollen analysis of core samples (G. Rouse, unpublished information) has shown that the lake so formed may have dried up but, after a period as woodland, later returned to its present form.

The lake today (Fig. 1) has a drainage area of approximately 6.5 km^2, rising to a maximum of 1000 m above the lake level. There is a very heavy run-off resulting from the heavy annual rainfall combined with a steep drainage basin, shallow soil, and extensive areas where the vegetation is recent regeneration growth, after logging and fire. These conditions combine to produce sudden increases in discharge of the inlet stream and resulting sudden rises in the lake level.

The lake itself is small, 800 m long and about 200 m across at the widest point (Fig. 2). The maximum depth is 7 m during a period of high water but usually it fluctuates between 5.5 and 6 m and the mean depth is 2.4 m. The area of the lake on April 13, 1963 was 13.33 ha (32.9 acres) and the volume 321,300 m^3; the volumes of areas between 1-m contours were:

Depth (*m*)	0–1	1–2	2–3	3–4	4–5	5–6	Total
Volume (*m*^{3})	133,300	90,300	43,800	31,300	16,500	6,200	341,400

During heavy spates the equivalent of the total volume of the lake may be flushed out in less than 2.3 days: at these times the surface of the water may rise as much as 1 m in 24 hr.

Much of the lake bottom has a sparse covering of macrophytes. In water below 2 m these are almost exclusively *Isoetes occidentalis* and over much of the rest of the lake the bottom is covered with two species of *Vallisineria*. Around the edges are beds of *Nuphar variagatum* and *Potamogeton natans*, which in places are gradually extending arms toward the middle of the lake as successional changes result in the gradual filling in of the lake. Surrounding the large spring, and one or two of the small springs are beds of *Chara*.

PHYSICAL AND CHEMICAL FEATURES OF THE LAKE

The chemical composition of the water reflects the fast run-off of the rain water, the igneous rocks, and the absence of deep soil in the drainage basin. Nutrient concentrations are particularly low as is typical of the mountain lakes in the Coast Mountains (Northcote and Larkin, 1963). The TDS was between 12 and 15 ppm. Very accurate chemical determinations were not possible, but those done (by General Testing Laboratories, Co. Ltd., Vancouver) showed the following ranges in ppm over eight samples: Na, 0.7–6.8; K, 0–0.5;

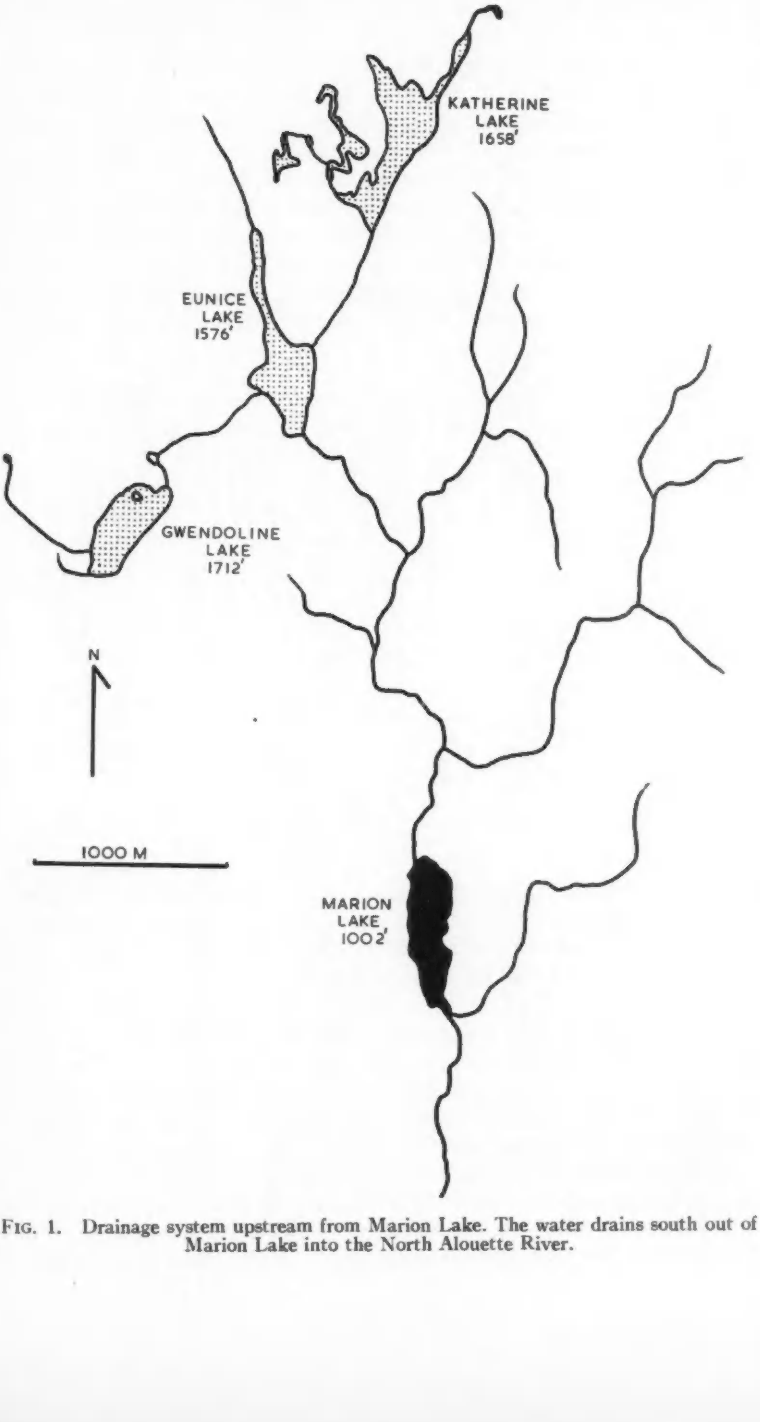

KATHERINE
LAKE
1658'
EUNICE
LAKE
1576'
GWENDOLINE
LAKE
1712'
N
1000 M
MARION
LAKE
1002'

FIG. 1. Drainage system upstream from Marion Lake. The water drains south out of Marion Lake into the North Alouette River.

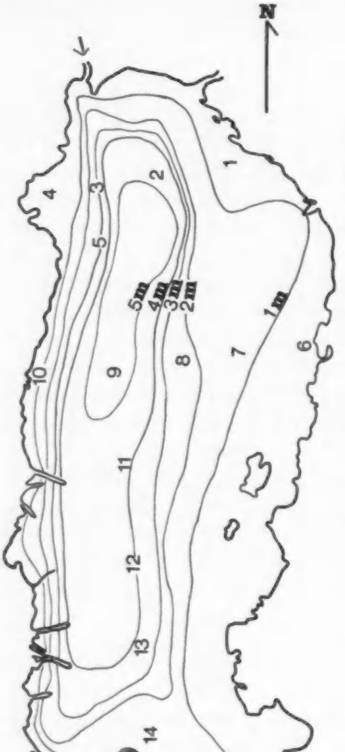

N
200m
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
5m
4m
3m
2m
1m
2m
1m
2m

FIG. 2. Marion Lake showing the depth contours in metres and the 20 stations used in the study. The main station is station 9.

Mg, <0.1–0.4; Ca, 2.6–25.5; Fe, 0.1–0.3; Si, 1.3–13.5; PO_4, <0.05–0.15; NO_3, <0.1–3.5; SO_4, 0.4–2.4; Cl, 0.7–2.4; CO_3, 0; HCO_3, 0.3–3.0.

There are a number of small springs in 2–3 m of water around the edge of the lake and one large spring just southwest of station 14 (Fig. 2). Measurement of the nutrients in this latter spring showed that they tend to be higher than those in the surrounding water; this was particularly true of calcium.

The shallow nature of the lake, its orientation along the direction of the prevailing winds, which come from the south, and the relatively high flushing rate all act to prevent permanent stratification in the summer months. During the period from mid-May to October the surface of water at station 9 is warmer than that near the bottom, sometimes reaching 24 C, but during the rest of the year there is complete mixing (Fig. 3). This is not the case, however, over the main spring, where during the summer months there is a very marked thermocline at about 1 m; the water temperature frequently changes from 20 C at the surface to 9.5 C in the spring water in a distance of 30–40 cm.

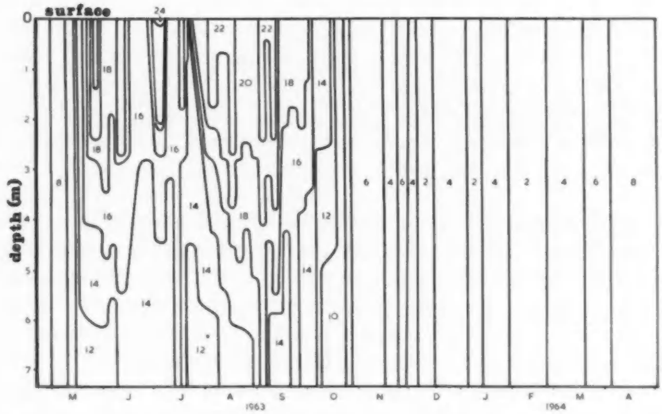


FIG. 3. Temperature pattern (C) for station 9 in Marion Lake for 1 year.

The lake may freeze for short periods in the winter and at other times it is covered with a layer of snow slush.

The hydrogen ion readings over a period of 1 year at all depths at station 9 and at other locations in the lake were between *p*H 6.3 and 7.4 although the usual range was 6.8–7.2. At the edge of the lake in the water surrounding the *Sphagnum* a *p*H as low as 5.8 was recorded. Oxygen and total free carbon dioxide were measured by titration at the lake side using the standard volumetric methods (American Public Health Association, 1960). In summer the oxygen in the water near the bottom mud decreased noticeably (Fig. 4) but during other times of the year the water column was well oxygenated throughout. The water in the largest spring resembled the inlet water in the amount

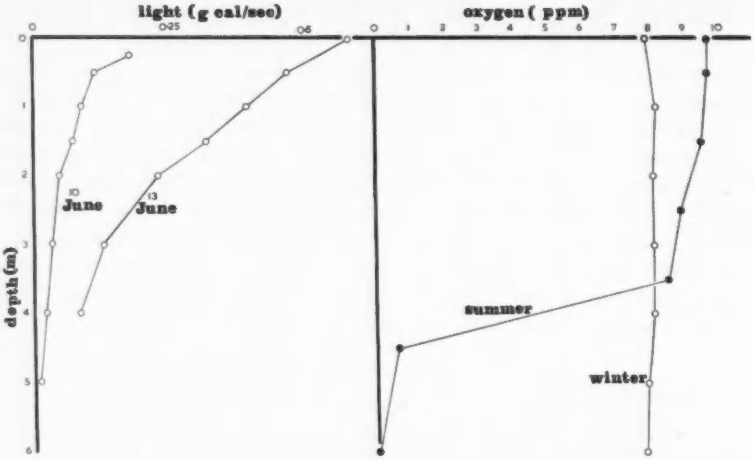


FIG. 4. *Left*, penetration of light on a bright (June 13) and a rainy (June 10) day in 1966. A subsurface photometer with a deck cell was used to make the measurements. *Right*, examples of midsummer and winter oxygen profiles at station 9 in Marion Lake.

of oxygen present. Titrations for total free carbon dioxide were not repeatable to within less than 10%. This reflected the very low levels of free CO_2 present and the lack of a really accurate field method. At the very low levels of free CO_2 present it was difficult to prevent contamination of the sample with CO_2 from the air and to be certain of the end point "a change from grey to bluish grey." The difference between individuals making the titrations in the point at which they could see this change was as high as 25% of the total acid added. The result over the year ranged between 5 and 15 mg of free CO_2 per litre. More recent readings using a portable *p*H-meter confirmed these observations. Carbonates were absent at all times.

The lake itself resembles a small acid bog lake in appearance and its bottom is completely covered with a deep flocculent ooze except around the springs and the inlet. The water is not acid but neutral and it is difficult to classify the lake as it is neither deep like the oligotrophic lakes above it in the same drainage basin system nor eutrophic like the lakes in the Fraser Valley below, which receive fertilizer-rich water from the surrounding farm land. The chironomid fauna is intermediate between the two extremes (Hamilton, MS, 1965).

METHODS

All observations were made in situ and, except where stated otherwise, were made in the deepest part of the lake at station 9. BOD bottles were suspended in overlapping 4 hr-periods throughout the time from dawn to dusk (i.e. down at 6:00 AM and up at 10:00 AM; down at 8:00 AM and up at

12:00 noon etc.). Usually observations were made on 2 consecutive days but on three occasions they were continued daily over a period of 10 days so that the variability in measurements of productivity within a period could be estimated. Except for two types of experiments, bottles were suspended at 1-m depth. These exceptions were when measurements of differences in productivity with depth were made and when comparison was made between different stations at the same time. In this latter case some of the stations were in very shallow water and therefore all bottles were hung at 0.5 m.

Samples were collected in a polyethylene sampling bottle and transferred to clean well-rinsed 300-ml BOD bottles via a polyethylene funnel which contained a No. 12 nylon plankton net (0.11-mm diam mesh hole) for the removal of the zooplankton. The sample was protected from the direct rays of the sun whilst at the surface by a black cloth bag over the bottle. Four microcuries of C^{14} in the form of $NaHCO_3$ were transferred from the ampoule to the bottom of the bottle using a 2-ml hypodermic syringe with a 4-inch needle. The ampoule was rinsed with water from the top of the bottle. After fixing the stoppers firmly with steel wire, the bottles were suspended from rings hung at the sample depth from a long, thin wooden bar floating on the surface. A dark bottle was hung 10 cm below the paired light bottles. After 4 hr, photosynthesis was stopped by the addition of 8 drops of 40% neutral formalin solution (Strickland and Parsons, 1960).

Filtration of 100, 150, or 300 ml of the sample was made at the lake side through AA Milipore filters (0.8-μ pore size) at a vacuum of 15 inches of mercury (Goldman, 1963). More recently Steemann Nielsen (1964), working on marine algae has suggested that if Millipore filters are used at a pressure above 5 inches of mercury, certain cells would break and some of their contents would be lost. C. R. Goldman (personal communication) has found that this was not the case in his study on freshwater algae. The filters were washed with a standard amount of water from a nearby spring and then air dried and stored in a desiccator.

The ampoules were obtained from the International Agency for C^{14} Determination in Denmark and all filters were returned to this agency for counting.

Two corrections were applied to all the measurements of primary productivity. All data were multiplied by 1.45 in accordance with the recent correction applied by the International Agency to all the results of their determinations. The second correction was for a further increase of 7.2% resulting from the use of AA rather than HA Millipore filters. Goldman (1963) has pointed out that some particulate material passes through AA filters and is stopped by the HA filters, whose pore size is 0.45 μ. The results of filtering 46 samples through both HA and AA filters are summarized in Table II.

The use of formalin to stop photosynthesis may burst the delicate nannoplankton cells and thus allow their contents to pass through the membrane filters. This would result in a lowering of the estimate of productivity. The alternative, however, is likely to bias the results in the other direction because

TABLE II. Comparison of productivity data using HA (0.45 μ) and AA (0.8 μ) Millipore filters. Units are Σ of mg C/m³ per hour of N observations.

Date	No. of observations (*N*)	Filter AA (0.8 μ)	 HA (0.47 μ)
May 22, 1964	19	0.978	1.032
June 11, 1964	11	1.864	2.346
July 2, 1964	16	8.724	8.856
		100%	107.18%

the bottles must be kept in complete darkness until they are filtered; otherwise photosynthesis is likely to continue and even if in complete darkness there might be a dark reaction that results in the continuous uptake of C^{14}. The results as presented here are not corrected in any way for the fact that formalin was used. Initial tests suggested that the error produced by adding formalin may be high (20%) but in these tests the bottles were not filtered immediately after exposure. D. Fillion (unpublished results) has repeated some of these tests and his results (from Kootenay Lake) suggest the use of formalin may reduce productivity estimates about 5%. The detrimental effect of using formalin may increase in lakes where most of the productivity is by nannoplankton.

The separation of the photosynthesis of nannoplankton (i.e. cells between 2 and 10 μ diam) from that of the rest of the phytoplankton was made by filtering half a sample through the Millipore and the other half through a 25 net (0.064 mm diam) before filtering it through the Millipore. It is assumed that almost all phytoplankton cells are removed from the sample in the latter case.

RESULTS

TEMPORAL DIFFERENCES IN PRODUCTION

Marion Lake phytoplankton was characterised by a very low level of primary productivity and a very short productive season (Fig. 5). The first signs of a change in the rate of carbon fixation occurred in late May. This was followed by a sharp rise in production to a peak in early July. Subsequently there appeared to be a drop in mid-July and a rise to another peak in August before productivity dropped down in November to the winter conditions of virtually no productivity. Thus during only 5 months in the year — June to October — was energy being fixed in any quantity by the phytoplankton. This short productive season must inevitably restrict the seasonal occurrence and possibly abundance of the zooplankton and the bottom fauna that feed on phytoplankton.

Differences in productivity between consecutive days were sometimes considerable (Fig. 5). This is illustrated by comparing the daily production

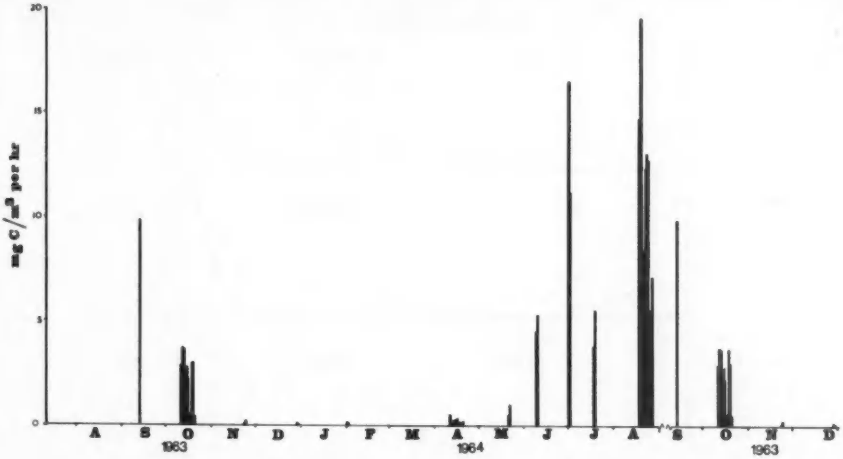


FIG. 5. Seasonal differences in primary productivity of the phytoplankton at 1-m depth, station 9 in Marion Lake. The 1963 data are repeated to show the shape of the pulse of production in the summer.

in the three 10-day periods. The means, ranges, and standard errors for these three periods (Table IV) show that a single day's measurement of productivity differed considerably from the mean productivity for that particular week.

This difference between days partly results from unexplained different shapes of the productivity curve within the days (Fig. 6). Despite the marked differences between days, the peak of production was usually during the afternoon and rarely at noon (1:00 PM daylight saving time).

SPATIAL DIFFERENCES IN PRODUCTION

The highest carbon fixation in Marion Lake was always at the surface and on no occasion was any "light inhibition" recorded at the surface. The productivity curve (Fig. 7) resembled closely the light extinction curve (Fig. 4). This was surprising considering the general occurrence of light inhibition in other studies and the transparency of the lake water.

The results from three experiments where productivity was measured simultaneously at 0.5-m depth at 20 locations in the lake show that production is by no means uniform at the same depth all over the lake. The results from the first experiment on June 10, 1964 (Fig. 8.) appeared to fit a clear pattern: production was highest near the inlet, particularly in the warmer shallow areas, then dropped towards the large spring, rose again between the spring and the outlet except in the still water area in the southeast corner. Similar experiments on July 23 and August 28, 1964 (Fig. 9) did not fit the same pattern except the line of stations between the inlet and the outlet, where there was

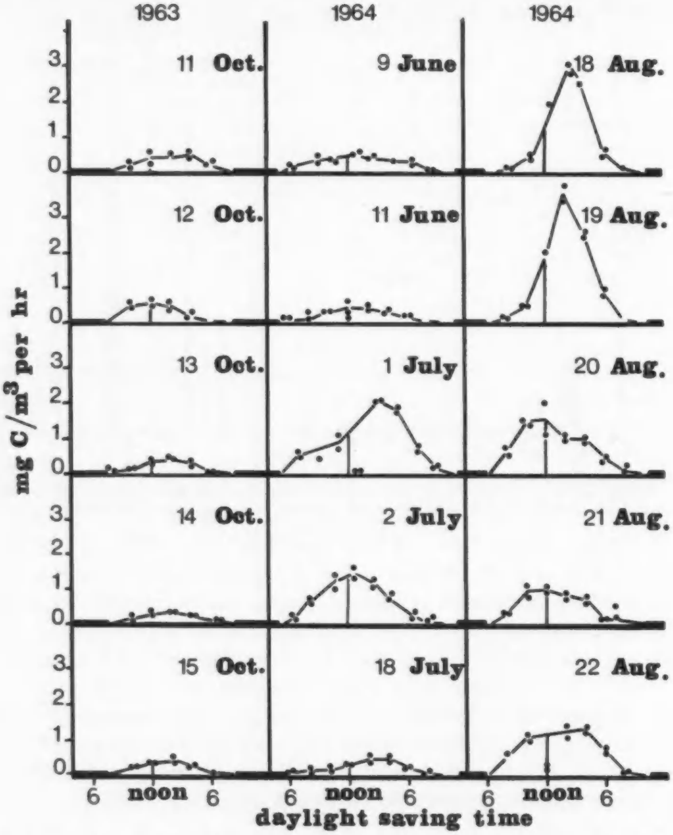


FIG. 6. Examples of dawn to dusk observations used to obtain the daily productivity given in Fig. 5. Each point is for a single bottle exposed for 4 hr at 1 m at station 9 in Marion Lake. The median time for the 4 hr is used. Celestial noon is at 1 PM.

a definite tendency for carbon-fixation to drop as one moves south down the lake as far as station 14 near the large spring. Between the spring and the outlet, production rose again, although on two occasions it dropped again at the outlet station (station 20).

DISCUSSION

THE C^{14} METHOD

The C^{14} method of measuring productivity in marine and lake phytoplankton is now a well-established method with clear-cut techniques (e.g. Goldmann, 1963; Steemann Nielsen, 1964). It is not always clear, however, what variation there is around a particular observation. If we measure, for example, the

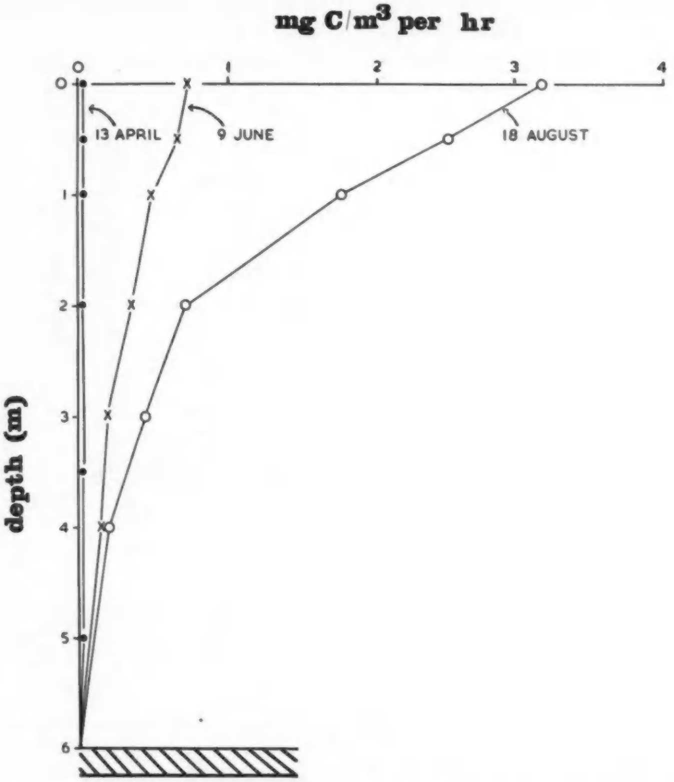


FIG. 7. Example of differences in productivity with depth at station 9 in Marion Lake.

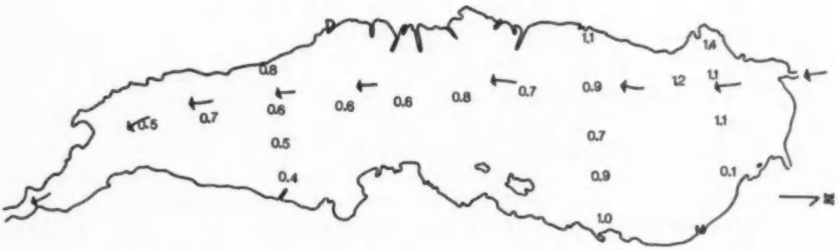

1.1
1.4
0.8
1.2
1.1
0.7
0.9
0.8
0.6
0.6
0.6
0.7
0.5
1.1
0.7
0.5
0.4
0.9
0.1
1.0
N

FIG. 8. Productivity (mg C/m^3 per hour) at a 0.5 m measured simultaneously at 20 stations in Marion Lake between 10 AM and 2 PM on June 10, 1964. Stations are identifiable from Fig. 2.

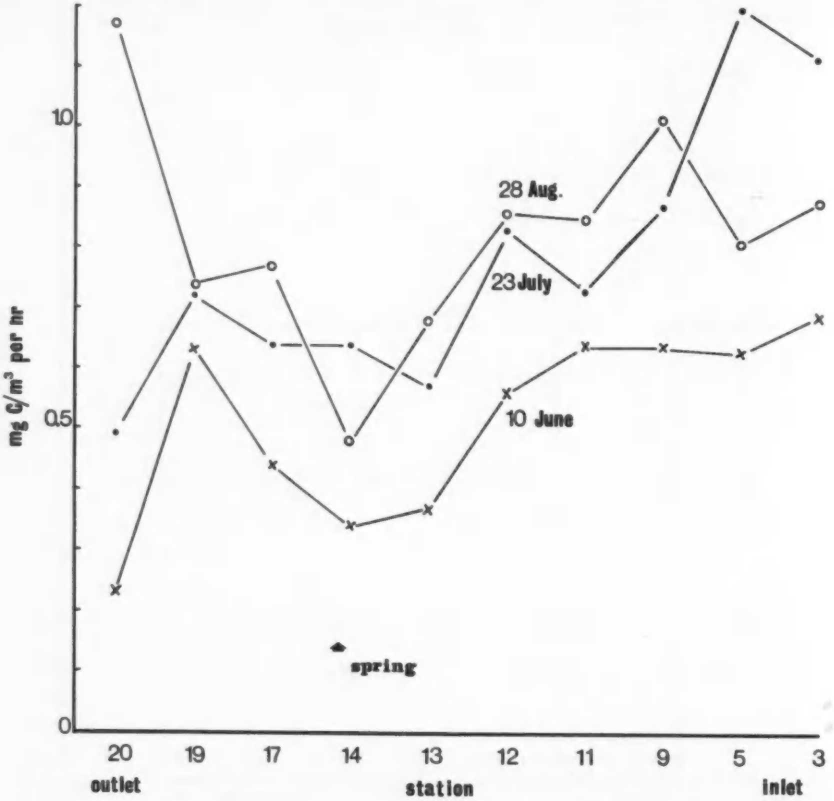


FIG. 9. Simultaneous productivity measurements made at 0.5-m depth on a line between the inlet and the outlet of Marion Lake. Station numbers refer to those given in Fig. 2. All measurements were made in 1964.

uptake in a pair of samples exposed at 1 m in a lake from 10:00 AM to 2:00 PM on one particular day, it would be interesting to learn with what degree of accuracy this tells us the total productivity for that day or the productivity on other days in that week, or the productivity in the lake as a whole at that depth. Furthermore, what does one of the replicates of a pair of bottles tell us about its partner? The results obtained in this present study can be examined with this problem of variability in mind.

VARIATION BETWEEN REPLICATE SAMPLES

So far little attention has been paid to the variations between replicate samples. We do not know if the accuracy of the C^{14} method is constant at different levels of productivity or whether it varies relative to the level of the productivity. To examine this point the differences between replicates in 279 pairs of samples for the whole year at 1 m were compared with the average productivities for the pairs (Fig. 10). The difference between replicates is obviously related to the level of uptake of the C^{14} by the phytoplankton. Whether this is a linear relationship cannot be established from the available data. One would imagine that above a certain level, not reached in Marion Lake, the relative accuracy of the method would remain constant.

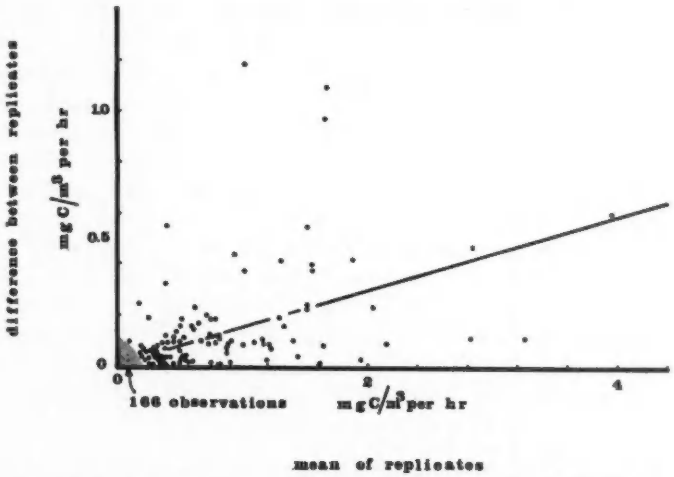


FIG. 10. Differences between in situ replicates (279 paired observations) made at different levels of productivity. There is a tendency for the difference to increase as the productivity level increases (r =0.568; b =0.14; F ratio = 131.4 with 277 df).

VARIATION BETWEEN DAYS

On three occasions measurements were made for 10-day periods with overlapping 4-hr exposures from dawn to dusk each day (e.g. Fig. 6). By comparing the data from these 10-day periods it was possible to get some estimate of the general production at the time of year concerned and the between-day variation. Reasons for the marked differences between days (Table III) were not determined. Goldman (1960) found that carbon fixation from photosynthesis was within 10% of being directly proportional to available light energy in Brooks Lake, Alaska. But light readings from the nearest recording station at the University of British Columbia, 50 miles to the west of Marion Lake, showed no association with light energy, although this may only reflect the light differences between the two localities. An association to explain the fluctuations in production could not be found with cloud cover recorded at the weather station near the lake, runoff (as rain on the previous day recorded

TABLE III. Variation in productivity (mg C/m³ per day) between days and between stations in Marion Lake in selected months.

Month and year	No.	Mean ± SE	Range	SD	Coefficient of variation	
			Between days, at 1 m			
October 1963	10	2.63 ± 1.57	0.50 +3.96	3.66	138.9%	137.5%
April 1964	10	0.27 ± 0.13	0.05 –0.56	0.41	153.1%	
August 1964	10	11.97 ± 4.57	5.84 –21.00	14.44	120.7%	
			Between stations, at 0.5 m			
June 1964	20	0.73 ± 0.27	0.12 –1.41	1.20	165.0%	143.5%
July 1964	20	0.79 ± 0.18	0.48 –1.17	0.81	102.2%	
August 1964	20	0.49 ± 0.18	0.23 –0.69	0.81	163.4%	

at the same station), lake depth, or temperature. Under the conditions of fluctuating cloud and rain of an oceanic climate such as found along the coast of British Columbia, a single observation gives very little information about the productivity of the phytoplankton for that week. Rhode et al. (1958) pointed out that weekly measurements were inadequate as a measure of temporal variation in productivity.

VARIATION WITHIN DAYS

It is now clear from a number of studies that productivity during the daylight hours does not usually follow a normal smooth curve with a peak at noon (or 1 PM during daylight saving time). At times production is at its highest at noon, when the maximum light energy is available; at other times the curve is skewed with maximum productivity in the morning (Vollenweider and Nauwerck, 1961), or in the afternoon as often occurred in this present study (Fig. 6). A morning peak might be due to the rapid depletion of nutrients during the day and the re-fertilization of the water in the photic zone by zooplankton which migrate to the surface the following night. One possible explanation for an afternoon peak would be that productivity is closely related to water temperature. During some windless sunny days in summer the surface water on Marion Lake rose as much as 4 degrees, which might influence photosynthetic rate (Fig. 11), but this explanation is not sufficient to explain the afternoon peaks, as the temperature of the surface water did not always rise during the afternoons when the peak productivity was in the afternoon (e.g. August 18, 1964 in Fig. 6).

In most studies it is now usual to expose the light and dark bottles for 4 hr (10:00 AM–2:00 PM) and from this to extrapolate the productivity for the whole day assuming a bell-shaped productivity curve with the peak at noon. In this study daily values from dawn to dusk were plotted against the measurements for the 4 hr about noon. (Fig. 12). There is a close relationship between the two ($r = 0.98$, $b = 0.1074$). The variation could be explained in large measure by the changes in day length.

VARIATIONS BETWEEN STATIONS

Just as there is the question "How accurately can tomorrow's productivity be predicted using today's data?" so there is the question "How accurately can the productivity at the same depth in other parts of the lake be predicted using the data from one standard station?" One might expect that there would be more deviation in the latter case as the levels of nutrients, oxygen, temperature, and light penetration, etc. can be changed by so many factors. In Marion Lake this problem was examined on three occasions when measurements were made with paired bottles hung at 0.5 m at 20 stations in the lake (Fig. 2). The variations between stations at one time (e.g. Fig. 8) are just about the same as between days at one station (Table IV).

VARIATIONS BETWEEN DEPTHS

The absence of surface inhibition (even on the sunniest days) is surprising and contrasts markedly with findings in other studies. Steemann Nielsen

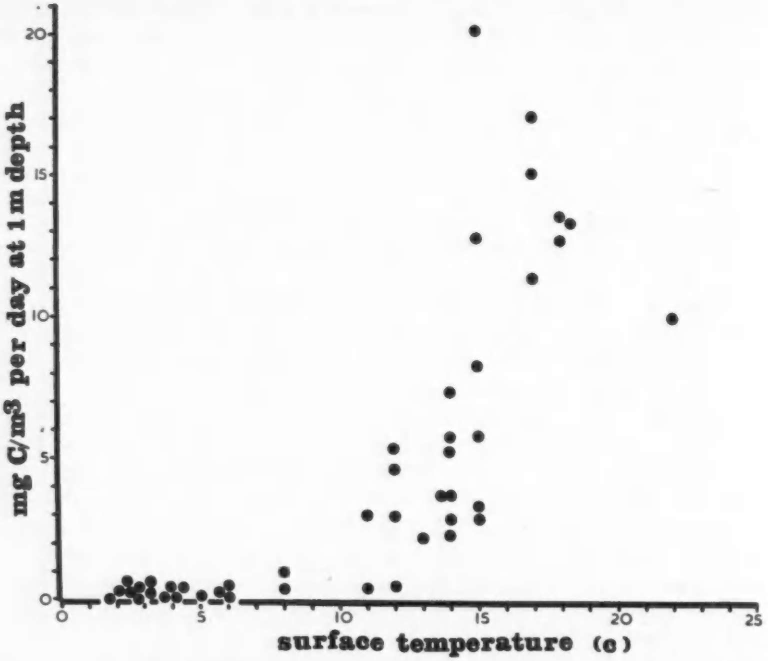


FIG. 11. Daily productivity measurements at 1 m at station 9 in Marion Lake (Fig. 5) plotted against surface water temperatures for the same days. There appears to be a threshold at 10 C above which productivity is linearly related to water temperature and below which little or no productivity takes place.

(1964) indicates maximum inhibition was 56% on very bright days and averaged around 5% although on very dull days there was no inhibitory effect. In Marion Lake the productivity has the same form as the light penetration curves (Fig. 4 and 7). Whether this type of productivity curve results from the low nutrient level or the mixing of the water is not known. One possibility is that there is light inhibition and that it extends down to the bottom, at 6 m, so that there are no subsurface optimal regions as one normally finds.

LOW PRODUCTIVITY IN MARION LAKE

The primary productivity of the phytoplankton of Marion Lake is very low in comparison with other temperate region lakes that have been studied. It closely resembles those recorded (Goldman, 1960) in the lakes of Alaska and the Canadian Arctic. Measurements from four of these lakes and one from Marion Lake made during the same week of the year contrast strikingly with those recorded from temperate eutrophic lakes (Table IV).

The primary reason for the low productivity is the very low nutrient level in the lake. A certain amount of evidence is available from the 20 station

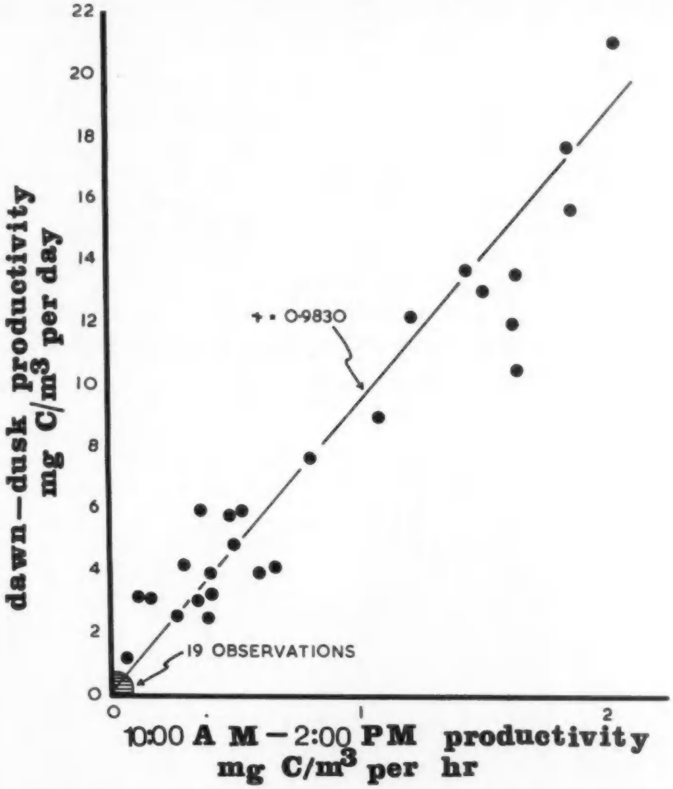


FIG. 12. Relationship between productivity measured by bottles exposed in situ between 10 AM and 2 PM and productivity measured by bottles exposed in situ for 4 hr every 2 hr from dawn to dusk. All measurements made at 1-m depth at station 9 in Marion Lake. It appears that the noon period exposure would give a reasonably close estimate of the daily productivity.

series to confirm that nutrients are a limiting factor in the lake. There seems to be only one similar feature in the data from the three occasions when the 20-station experiment was run; this was the consistent drop in productivity down the central row of stations from the inlet and the rise after the water passes the large spring. The water from the spring was found to be higher in nutrients than the lake inlet water (e.g. September 14, 1963, inlet calcium 7.65 ppm; spring water calcium 25.5 ppm), and it can be assumed that the spring acts continuously to fertilize the low end of the lake. The explanation for the generally low level of nutrients in the water of the region lies in a combination of the heavy rainfall (240 cm per year average), the insoluble granite rocks, and the resulting fast run-off. The fact that much of the water-shed

TABLE IV. Comparison of primary productivity in Marion Lake and in arctic and temperate lakes.

Lake	Latitude	Date	mg C/m³ per day at 1 m	Reference
Marion, British Columbia	49°19′	Aug. 20, 1964	14.60	
S-7, Southampton Island	63°36′	Aug. 13–19	2.90	Goldman, 1960
Brooks, Alaska	58°30′	Aug. 22	1.96	"
Naknek, Alaska	58°30′	Aug. 19	10.42	"
Becharof, Alaska	58°00′	Aug. 23	0.63	"
Clear, California	39°00′	July 28, 1960	ca. 114	Goldman and Wetzel, 1963
Tystrup Sø, Denmark	55°22′	Aug. 19, 1959	1270	Kristiansen and Mathiesen, 1964
Esrom Sø, Denmark	56°00′	Aug. 20, 1956	ca. 375	Jonasson and Mathiesen, 1959
Furesø, Denmark	55°48′	Aug. 3, 1956	ca. 1900	Jonasson and Mathiesen, 1959

was logged and burnt in the last 30 years means that the run-off is faster than it would be under natural virgin forest conditions.

The very low level of nutrients in the lake will obviously set an upper limit to the phytoplankton productivity but this upper limit will only be reached if the phytoplankton can utilize the nutrients to the fullest extent. It seems reasonable to assume that nutrients are available at all times during the year in the inlet water. But the annual productivity curve (Fig. 5) indicates that productivity is limited to a narrow period of 5 months in summer and that the phytoplankton does not utilize the available nutrients at other times, such as in the spring. Is productivity in the lake limited by lack of sufficient light in spring and autumn? To examine this point, the daily light readings made on the University of British Columbia campus, 50 km to the west but within the general climatic area (Fig. 13), were compared with production figures (Fig. 5). A comparison of these two curves shows that although of the same general shape, light is certainly available in spring and less so in autumn (Fig. 14) at a time when production is low. If light is not limiting it suggests that something else is preventing the phytoplankton from fully utilizing the available nutrients in the water.

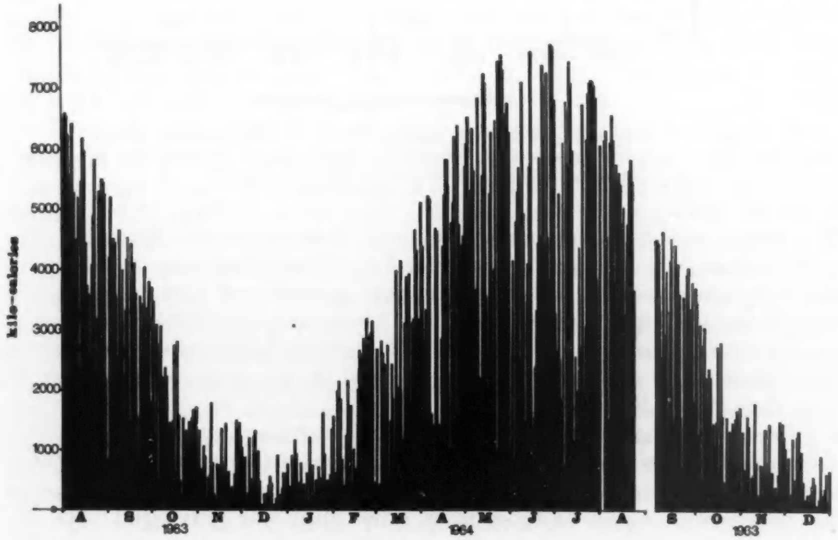


FIG. 13. Sunlight measured at the University of British Columbia campus weather station in Vancouver (from weather records 1963 and 1964). 1963 data repeated to show shape of curve for year. Compare with Fig. 5.

As the lake does not warm up until May it is possible that the temperature affects the level of production. This certainly seems to be the case as plotting surface temperature against productivity gives a close relationship (Fig. 11).

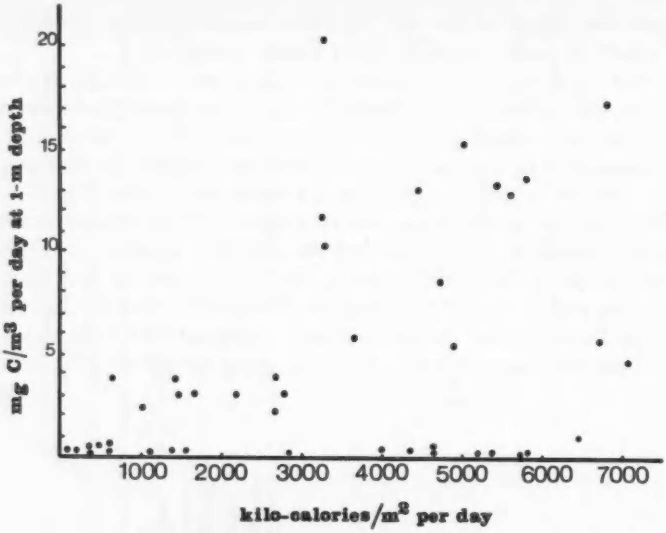


FIG. 14. Comparison of sunlight readings (Fig. 13) with productivity on the same days at 1 m at station 9 in Marion Lake (Fig. 5). A comparison of temperature and productivity is given in Fig. 11.

The heavy run-off in the spring, frequently from snow melt, keeps the lake from warming up until late in the year. This limits production to a 5-month pulse in summer which ends with the cold weather and cold run-off water from increasing rainfall in the autumn. In October 1963 observations were made over a 10-day period coinciding with this drop in lake temperature, which came when heavy cold rains caused dilution of the standing crop and resulted in a drop in productivity.

It is clear that flushing must also play an important part in reducing the productivity in Marion Lake although this does not seem to be as important as the temperature. Productivity, measured in an area of open water, was not increased in winter at times when snow cover was heavy and both the flushing and grazing rates were very low. The tendency for productivity to be higher near the edges of the lake (Fig. 8) is probably a combination of higher temperatures and a reduced flushing of the standing crop at the edges.

It is usually accepted that phytoplankton can adapt to almost any natural lake conditions and particularly to low temperatures (Fogg, 1965). In fact it has been frequently shown that certain species adapt to maintain a relatively high level of productivity under a thick ice cover (Goldman, 1963). Why has this not occurred in Marion Lake? First, it may be that the adaptation has taken place but that because of high flushing rates the species do not realize their potential. This cannot always be the case, however, because during heavy snow cover the flushing rate is low. An alternative explanation is that early spring blooms are associated with certain species of diatoms. In Marion Lake productivity throughout the year is almost entirely (95%) by nannoplankton that pass through a No. 25 net (0.064-mm diam mesh hole) and any increase of spring bloom in the diatom populations does not appear to significantly change production. A third alternative is that the bloom was of short duration and not recorded by the sampling. Studies now in progress may provide an answer to the lack of adaptation of phytoplankton to low temperatures.

The regular stream- and wind-generated turnover of the water in the lake suggests that nutrients released by bacterial breakdown of the bottom mud would regularly fertilize the nutrient poor water. This is apparently not the case. One interpretation is that the mud is not being broken down to any significant extent. Hayes and Anthony (1959) showed that bacterial numbers were closely correlated with alkalinity. In Marion Lake the alkalinity is extremely low and therefore the standing crop of bacteria would be expected to be very low. Low water temperature through much of the year plus very low bacterial numbers would reduce detritus breakdown considerably, which would explain the very deep mud deposits (8 m) laid down since glaciation only 11,000 years ago and it would also partially explain why despite regular lake turnover the nutrient level remained very low.

The efficiency of the phytoplankton in converting light energy was calculated. Fifty per cent of the light available in the region (Fig. 13) over one year was assumed to be in the wavelengths for photosynthesis (Edmondson, 1955; Ryther, 1955) and 95% of the light was assumed to penetrate the surface of the water (Ryther, 1956). It was also assumed about 20% of the light penetrated to 2.4 m, the average depth of the lake (Fig. 4). This gave the available light energy as 100,435 Kcal/m^2 per year. The average annual productivity for the lake was estimated as 8.034 g C/m^2 per year which was assumed (Ryther et al., 1958) to be equivalent to 88.374 Kcal. This gives an efficiency of conversion of light energy by the phytoplankton of 0.0009%, an extremely low efficiency for natural situations. In fact, one wonders whether the lake energy budget is very much affected by this small pulse of phytoplankton energy in the summer or whether most of the lake's energy is derived from the macrophytes which cover much of the lake's bottom or the detritus which enters the lake in the inflow streams. Further studies are designed to answer this question.

One is tempted to speculate how the productivity could be increased. Artificial fertilization of the lake might have some effect during the months of May to September but at other times during the year the low temperatures and high flushing rate would make fertilization ineffective. An alternative would be to dam this lake. This would not only increase the volume and thereby reduce the flushing effect of spates on the standing crop but it would also result in an increase in lake temperature and increased productivity.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of William A. Shearer, a graduate student whose research on Marion Lake was halted by his untimely death in a diving accident.

I am grateful for the help I received from a number of other students, particularly P. Healey, A. L. Hamilton, J. A. Mathias, and G. Davies. Drs Glen Geen and T. G. Northcote were kind enough to criticise the manuscript.

Financial support was granted by the National Research Council of Canada.

REFERENCES

American Public Health Association. 1960. Standard methods for the examination of water and wastewater. 11th ed. American Public Health Association, Washington, D.C.

Armstrong, J. E. 1957. Surficial geology of New Westminster map-area, British Columbia. Geol. Surv. Canada, Paper 57–5, 1-25, and map 16-1957.

Canada, Department of Transport, 1963 and 1964. Meteorological branch, monthly record, meteorological observations in Canada. Queen's Printer, Ottawa, Canada.

Edmondson, W. T. 1955. Factors affecting productivity in fertilized salt water. Deep-Sea Res., 3 (Suppl.): 451–463.

Fogg, G. E. 1965. Algal cultures and phytoplankton ecology. University of Wisconsin Press, Madison and Milwaukee, Wisc.

Goldman, C. R. 1960. Primary productivity and limiting factors in three lakes of the Alaska Peninsula. Ecol. Monographs, **30**: 207–230.

1963. The measurement of primary productivity and limiting factors in fresh water with carbon-14. *In* M.S. Doty [ed.] Proceedings conference on primary productivity measurement, marine and freshwater. U.S. Atomic Energy Comm. T10-7633. p. 103–113.

Goldman, C. R., and R. G. Wetzel. 1963. A study of the primary productivity of Clear Lake, Lake County, California. Ecology, **44**: 283–294.

Hamilton, A. L. MS, 1965. An analysis of a freshwater benthic community with special reference to the Chironomidae. Ph.D. Thesis. University of British Columbia, Vancouver, B.C.

Hayes, F. R., and E. H. Anthony. 1959. Lake water and sediment. VI The standing crop of bacteria in lake sediments and its place in the classification of lakes. Limnol. Oceanog., **4**: 299–315.

Jonasson, P. M., and H. Mathiesen. 1959. Measurements of primary production in two Danish eutrophic lakes, Esrom Sø and Furesø. Oikos, **10**: 137–167.

Kendrew, W. G., and D. Kerr. 1955. The climate of British Columbia and the Yukon Territory. 1-222. Queen's Printer, Ottawa, Canada.

Kristiansen, J., and H. Mathiesen, 1964. Phytoplankton of the Tystrud-Bavelse Lakes, primary production and standing crop. Oikos, **15**: 1–43.

Northcote, T. G., and P. A. Larkin. 1963. Western Canada. *In* D. G. Frey [ed.] Limnology in North America. University of Wisconsin Press, Madison, Wisc. p. 451–485.

Nalewajko, C. 1966. Photosynthesis and excretion in various planktonic algae. Limnol. Oceanog., **11**: 1–10.

Orloci, L. MS, 1964. Vegetational and environmental variations in the ecosystems of the coastal western hemlock zone. Ph.D. Thesis. University of British Columbia, Vancouver, B.C.

Roddick, J. A., and J. E. Armstrong. 1956. Pitt Lake (Vancouver, east half) map. New Westminster District, British Columbia. Geol. Surv. Canada, map 8–1956.

Rhode, W., R. A. Vollenweider, and A. Nauwerk. 1958. The primary production and standing crop of phytoplankton. *In* A. A. Buzzati-Traverso [ed.] Perspectives in marine biology. University of California Press, Berkeley, Calif. p. 299–322.

Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanog., **1**: 67–70.

RYTHER, J. H., C. S. YENTSCH, E. M. HULBERT, AND R. R. VACCARO. 1958. The dynamics of a diatom bloom. Biol. Bull., **115**: 257–268.

STEEMANN NIELSEN, E. 1964. Recent advantages in measuring and understanding marine primary production. J. Animal. Ecol., **33**: 119–130.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1960. A manual of sea water analysis. Bull. Fish. Res. Bd. Canada, No. 125. 185 p.

VOLLENWEIDER, R. A., AND A. NAUWERCK. 1961. Some observations on the C^{14} method for measuring primary production. Verh. Intern. Ver. Limnol., **14**: 134–139.

WATT, W. A. 1966. Release of dissolved organic material from the cells of phytoplankton populations. Proc. Roy. Soc. London, Ser. B, **164**: 997, 521–551.

An Audiogram of the Atlantic Cod, *Gadus morhua* L.[1,2]

By Udo Buerkle

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Auditory thresholds were determined by means of a conditioned response to sound stimuli at frequencies 17.6, 35.3, 70.7, 141, 283, and 400 cycles/sec for 10 cod, *Gadus morhua*. The conditioned response was a change of cardiac rhythm. It was established through an electric shock as unconditioned stimulus, and could be monitored on an oscilloscope.

The thresholds indicated cod to have high sensitivity to sounds up to 283 cycles/sec. At 400 cycles/sec they were relatively deaf. Background noise in the experimental tank was high enough to influence thresholds; an absolute threshold could therefore not be determined.

INTRODUCTION

Although audiograms of marine teleosts have been determined for a number of species (Tavolga and Wodinsky, 1963), none have been determined for the Atlantic cod *Gadus morhua* L. or other species of the North Atlantic. Cod are non-ostariophysan teleosts with unspecialized ears. Unlike the ostariophysan teleosts which are noted for their high auditory sensitivity, they have no Weberian ossicles to connect the swim bladder to the inner ear. Nor do they have other apparent adaptations to increase auditory sensitivity, such as extensions of the swim bladder to the inner ear, which are found in some non-ostariophysan species. This study presents an audiogram of the Atlantic cod. It employs a change in cardiac rhythm as a conditioned response to pure sound stimuli at frequencies of 17.6, 35.3, 70.7, 141, 283, and 400 Hz.

MATERIALS AND METHODS

Experimental Animals

The cod were captured in Passamaquoddy Bay, N.B., by otter trawl. They were brought to the St. Andrews' laboratory and were kept in tanks in aerated running water (with a flow of approximately 10 liters per min) for 3 weeks before use in experiments. During this time they were acclimated at 8 C and were fed a mixture of beef liver and herring every 2nd day. Care was taken to use only fish in apparently good condition for experiments.

---

[1] Received for publication May 23, 1967.

[2] Based on a thesis submitted by the author in partial fulfilment of the requirements for the degree of Master of Science from McGill University, Montreal, P.Q.

J. Fish. Res. Bd. Canada, 24(11), 1967.
Printed in Canada.

DESCRIPTION OF EQUIPMENT

Thresholds were determined in a specially designed cement tank, 300 × 150 × 120 cm, with non-parallel sides and a sloping bottom. When sound is produced in the smaller end, the reflections of sound off the non-parallel sides and sloping bottom are propagated along the tank to the larger end. Reflections from this end are reduced by wedge-shaped blocks of Insulcrete (a special mixture of cement and sawdust (Albers, 1965)). The tank rested on a 1.25-cm thick Tico-mat (James Walker and Co. Ltd., Surrey, England) which insulated it to some extent from vibrations transmitted through the foundations (Fig. 1).

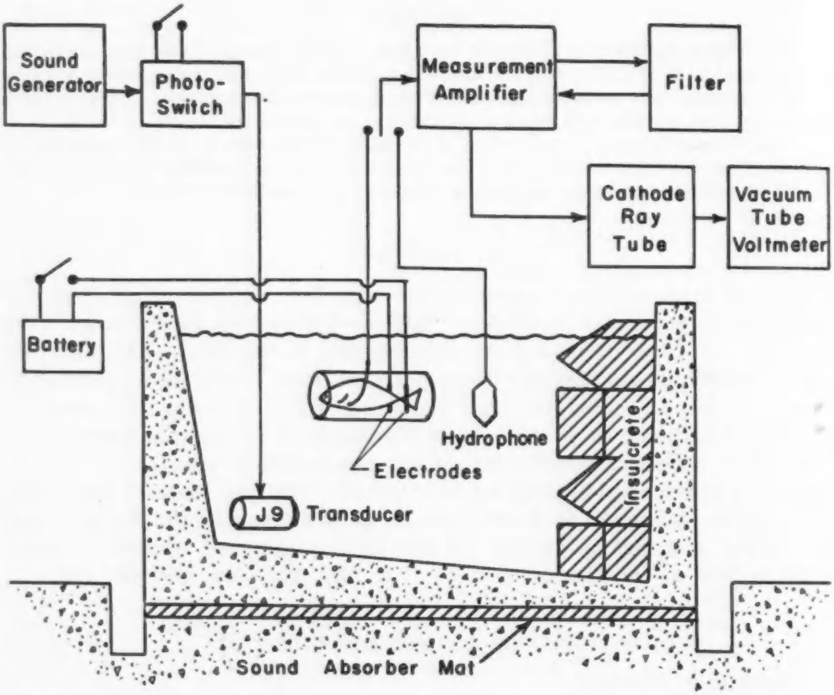

Sound Generator
Photo-Switch
Measurement Amplifier
Filter
Cathode Ray Tube
Vacuum Tube Voltmeter
Battery
Hydrophone
Electrodes
J9
Transducer
Insulcrete
Sound Absorber Mat

FIG. 1. Block diagram of instrumentation and crosssection of experimental tank.

Sound was produced with an audio generator (Hewlett-Packard Model 205AG) connected through a photoelectric switch to a wide band transducer (Chesapeake Instrument Corp. Model J9). The transducer was suspended in the smaller end of the experimental tank, and pointed diagonally across it. The sound pressure measurement system consisted of a ceramic hydrophone, a measurement amplifier (Eastech Ltd.), a band pass filter (Allison Model 2AB), an oscilloscope (Tektronix Model 503), and a vacuum tube voltmeter

(Ballantine). Cardiac rhythm of experimental animals could also be monitored on the oscilloscope.

CALIBRATION OF TANK

Background noise in the experimental tank was measured in frequency bands of 0–25, 25–50, 50–100, 100–200, 200–400, and 400–800 Hz. The mean pressure level in each band and its 95% fiducial limits were calculated.

Because it is desirable to determine thresholds at frequencies easily related to background noise, the geometric midpoints of the noise bands, except in band 0–25 Hz, were used as test frequencies. No geometric midpoint can be calculated between 0 and 25 Hz, therefore the frequency 17.6 Hz was chosen to represent noise band 0–25 Hz. Thus thresholds were to be determined at frequencies 17.6, 35.3, 70.7, 141, 283, and 566 Hz. Later, 400 Hz was added to the series because 566 Hz was found to be above the upper frequency limit of perception of cod.

The background noise pressure levels and their 95% fiducial intervals were converted to 1-Hz band levels (Table I) and are plotted at the test frequencies (Fig. 2).

When pure tone or noise in narrow frequency bands is produced under water in small tanks, reflections off the tank walls and off the surface and bottom of the tank cause a stationary pattern of high and low sound pressures called "standing waves" to form in the tank. This also occurred in this experiment when sound of the test frequencies was produced. To determine auditory capacities accurately it is necessary to have uniform sound pressure around experimental animals. Various methods of eliminating or reducing standing waves are recommended in the literature. Among them are the lining of tanks with rubberized horsehair (Tavolga and Wodinsky, 1963, 1965) and with styrofoam (Moore and Newman, 1956), and the use of sponges as sound absorbers (Wisby et al., 1964). These methods were ineffective in the present study. Within the pattern of high and low sound pressures of the standing waves in our experimental tank, however, small areas of relatively uniform sound pressure could be found at each test frequency.

One such area was located for each test frequency by systematically determining and plotting the pressure levels that occurred throughout the tank at the 30-cm depth. For frequencies 35.3, 70.7, 283, and 400 Hz, the pressure variation in the selected area was only ±0.5 db; for frequencies 17.6 and 141 Hz the variation was ±1 db. Sound pressures at the test frequencies were measured for varying attenuations of the sound-producing system in the appropriate area for each frequency. This allowed the production of sound at known levels, controlled by the attenuation of the sound-producing system.

By confining fish to the selected area of uniform pressure for each frequency to be tested, an accurate control over the sound pressure levels presented to it at each test frequency could be obtained.

EXPERIMENTAL PROCEDURE

Each fish was prepared to obtain an electrocardiogram by inserting a small stainless steel electrode with a fine insulated lead wire attached to it

TABLE I. Background noise in experimental tank and average auditory thresholds of 10 cod.

Noise band	Avg noise levels ±95% f.i.[a]	Avg noise levels in 1 Hz bands ±95% f.i.	Test frequencies to represent noise bands	Avg thresholds ±95% f.i. at test frequencies	Particle displacement of avg threshold
Hz	*db (re: 1 μ bar)*	*db (re: 1 μ bar)*	*Hz*	*db (re: 1 μ bar)*	Å
0–25	−15.3±3.3	−29.3±3.3	17.6	−5.2± 0.5	49.36
25–50	−14.2±3.5	−28.2±3.5	35.3	−0.8± 1.6	15.56
50–100	−8.3±1.5	−25.3±1.5	70.7	+0.4± 1.9	5.25
100–200	−7.6±1.8	−27.6±1.8	141	+1.3± 1.4	1.84
200–400	−19.0±1.8	−42.0±1.8	283	−4.6± 1.6	.37
	−18.4±4.1[b]	−46.2±4.1	400	+18.5±10.4	2.23
400–800	−24.3±8.7	−50.3±8.7	566	–	–

[a] f.i. = fiducial interval.

[b] When it was found that 566 Hz was above the upper frequency limit of perception of cod, the test frequency 400 Hz was introduced into the series. Since background noise was not measured in a band centred at 400 Hz, the noise levels in bands 200–400 and 400–800 Hz were averaged for comparisons of the threshold at 400 Hz to background noise.

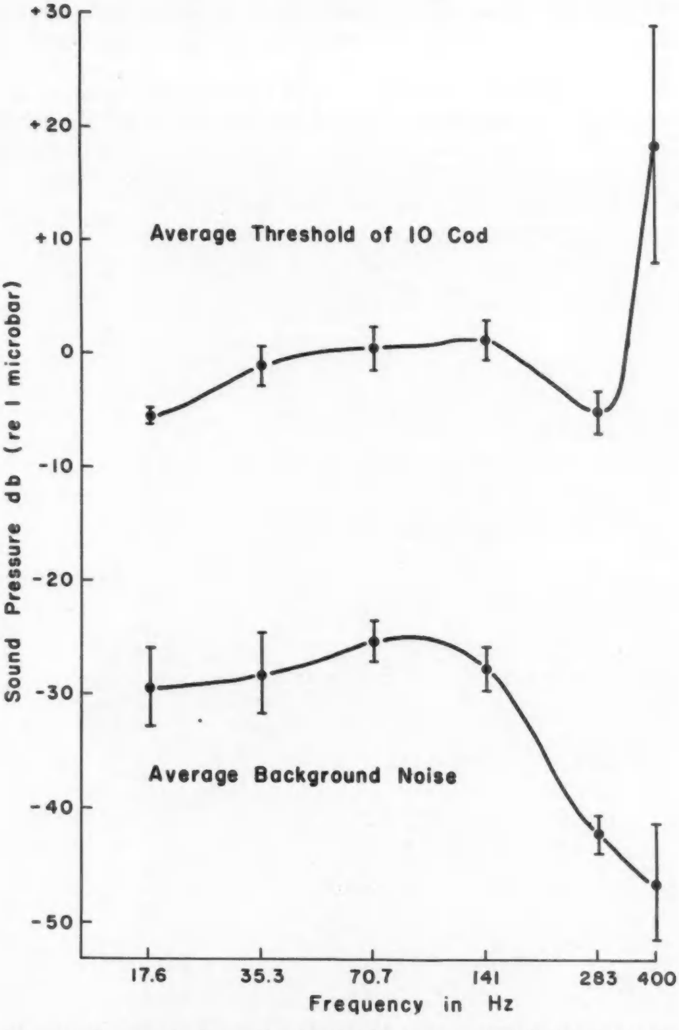


FIG. 2. Average background noise in 1 Hz bands with 95% fiducial limits plotted at test frequencies together with the average thresholds of 10 cod and their 95% fiducial limits.

through the pericardial cavity ventral to the ventricle. In this position the electrode picked up ventricle action potentials.

To confine a fish to the areas of uniform pressure during experiments, the "wired" fish was put in a cylindrical plastic screen cage just larger than the fish itself (Fig. 3). A pair of electrodes was attached to the cage so that an unconditioned stimulus of 6 v d-c could be applied to the caudal peduncle of the fish within.

The caged fish was suspended in the experimental tank in an area of uniform pressure. Its heartbeat was observed on the oscilloscope. If the electrocardiogram indicated that the electrode had been placed correctly, the fish was left overnight to allow it to recover from the operation of inserting the electrode before conditioning was begun.

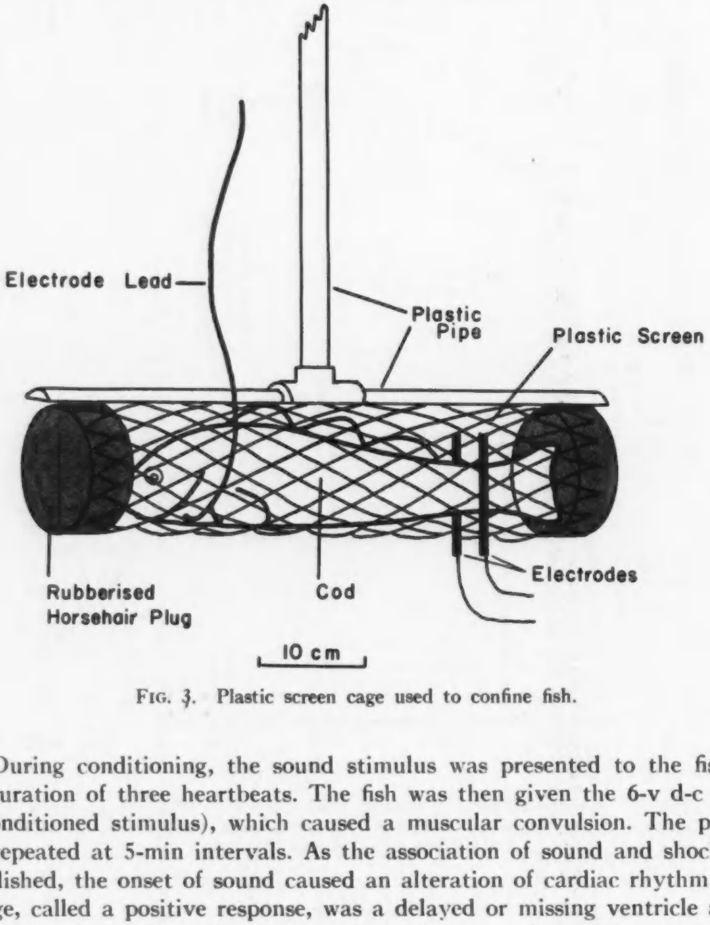


FIG. 3. Plastic screen cage used to confine fish.

During conditioning, the sound stimulus was presented to the fish for the duration of three heartbeats. The fish was then given the 6-v d-c shock (unconditioned stimulus), which caused a muscular convulsion. The process was repeated at 5-min intervals. As the association of sound and shock was established, the onset of sound caused an alteration of cardiac rhythm. This change, called a positive response, was a delayed or missing ventricle action potential and could be observed on the oscilloscope. It usually occurred on the second or third heartbeat after the onset of sound. A negative response was one in which no change in cardiac rhythm in response to a sound stimulus could be observed (Fig. 4).

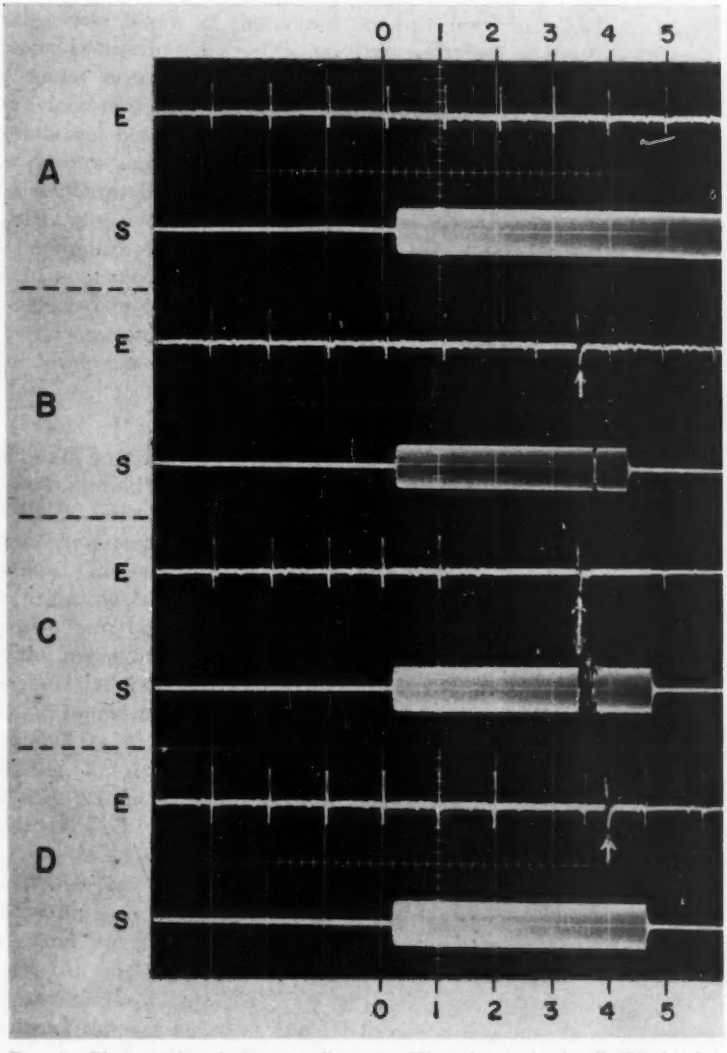


FIG. 4. Photographs of electrocardiograms (E) and sound stimuli (S) showing typical responses: A, a negative response; B, a delay of .6 cm of the second heartbeat after the onset of sound; C, a miss of the second heartbeat; D, a delay of .6 cm of the third heartbeat after the onset of sound. Arrows mark artifacts caused by the unconditioned stimulus.

When five consecutive positive responses were obtained, the training was regarded as complete. In subsequent testing the fish was given a reinforcing shock after both positive and negative responses to prevent extinction of the response.

Testing was begun at the sound pressure level at which training had taken place. It attempted to elicit positive responses of the fish to ever decreasing sound pressures, and entailed decreasing, and sometimes to confirm a previous response, increasing sound pressures by steps. As in training, a 5-min interval between presentations was maintained.

The process was continued until the responses of the fish at two levels of sound pressure, 1 db apart, could be separated. The upper level had to induce three positive responses before three negative ones, and the lower level had to induce three negative responses before three positive ones. Since a threshold is defined as that stimulus intensity at which a positive response can be expected in 50% of the presentations (Stevens, 1961), the threshold in these experiments is the sound pressure level midway between the upper and lower levels referred to above.

RESULTS AND DISCUSSION

The use of a change in cardiac rhythm as a conditioned response to sound stimuli allowed rapid training of cod. Few stimulus presentations were required to train them. Nine presentations were required to train one cod, two cod required seven presentations, two required five, and two required only two presentations. One cod did not require any training at all. It gave positive responses from the first stimulus presentation. This suggests that the absence or delay of a heartbeat could be a natural fright reaction which the electric shock of the unconditioned stimulus augments.

Thresholds at frequencies 17.6, 35.3, 70.7, 141, 283, and 400 Hz were determined for 10 cod ranging in length from 37 to 48 cm (Fig. 5). The average threshold and its 95% fiducial interval were calculated at each frequency (Table I, Fig. 2). Attempts to determine thresholds at 566 Hz were made with two cod, No. 5 and No. 6, because their thresholds did not show a sharp rise at 400 Hz. Cod No. 5 showed a rise of only 3 db (at 400 Hz); cod No. 6 showed a rise of 13 db over the threshold at the preceding frequency (283 Hz). Except for No. 3, all other cod showed a rise of over 17 db. Cod No. 3 did not form an association with sound at 400 Hz at more than +30 db (re 1 microbar), and was tested at 337 Hz, approximately midway between 283 and 400 Hz. At this frequency its threshold showed a rise of 24 db over the threshold at 283 Hz.

Neither of the cod tested at 566 Hz formed a response to this frequency at +35 db (re 1 microbar). This, together with the sharp rise in threshold of all other cod at 400 Hz, indicates that the upper frequency limit of sound perception in cod is near 400 Hz.

A comparison of the audiogram of cod with audiograms of other species is difficult because of differences in methods. The work of Tavolga and Wo-

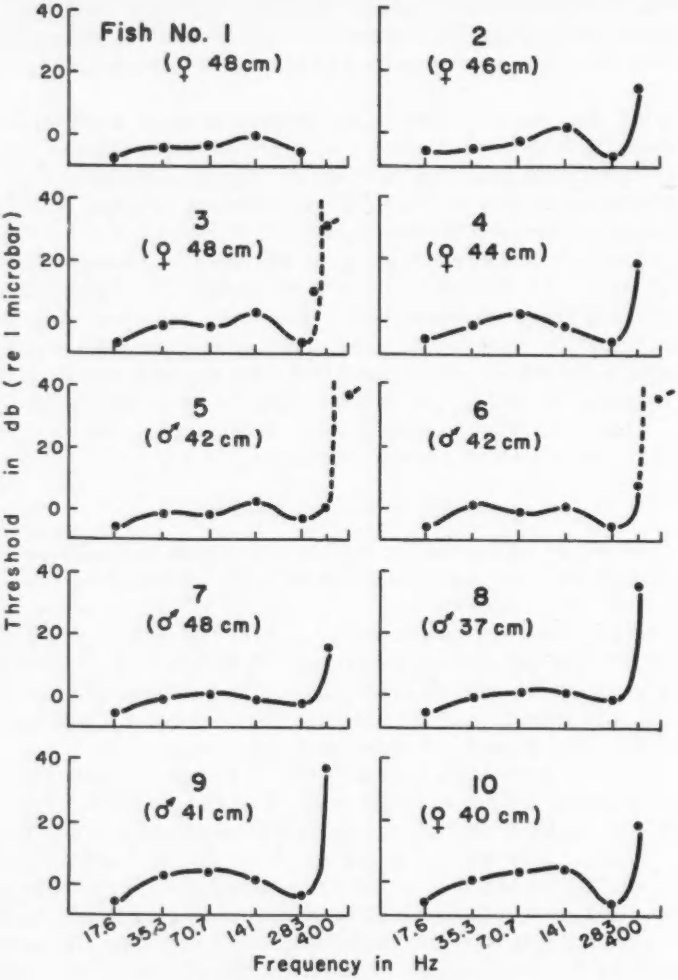


FIG. 5. Audiograms of 10 cod.

dinsky (1963) is the most comprehensive. It describes auditory capacities of nine marine teleosts from the Caribbean, all of which are non-ostariophysan. Their thresholds ranged between −17 and +28.2 db (re 1 microbar) at 100 Hz, and up to 42.7 db (re 1 microbar) between 1000 and 2400 Hz. Every species showed increased sensitivity somewhere between 200 and 800 Hz. At these most sensitive portions of the spectra, thresholds ranged from −39.8 to +16 db (re 1 microbar).

Major differences between the threshold of cod and those of the species tested by Tavolga and Wodinsky are apparent. Firstly, cod are insensitive to frequencies above 400 Hz, whereas the other species can hear above 1000 Hz. Secondly, the most sensitive part of the auditory spectrum of cod (in terms of pressure at least) occurred at the lower frequencies, whereas in the other species it occurred near the middle of the range. Whether these differences are due to inherent capacities, or to the difference in methods remains unanswered.

A suspected effect of size of fish on threshold proved to be insignificant at the 95% level for all frequencies except 400 Hz. However, the slope of the regression of threshold on size was negative at all frequencies. Thresholds showed a decrease of .12, .14, .41, .25, .14, and 2.21 db for an increase in length of 1 cm for frequencies 17.6, 35.3, 70.7, 141, 283, and 400 Hz respectively.

In recent experiments (Enger, 1966) it was shown that threshold pressure levels of goldfish decrease with decreasing distance between fish and sound source. If pressure were the actual stimulus perceived by the fish, there should be no such decrease. This suggests that sound pressure is not the stimulus perceived by the fish. However, for each frequency the particle displacement amplitude associated with the sound pressure at threshold level remained approximately the same at different distances between fish and source. Enger (1966) therefore suggests that displacement would be a better parameter than pressure in determinations of auditory thresholds in fish, particularly in laboratory experiments in which small aquaria are used.

In the present experiment thresholds were determined in a tank which was small relative to the wavelength of the frequencies tested. A calculation of displacement at threshold levels therefore seemed warranted.

When sound is produced under water, two types of displacement are created. The first is displacement caused by vibrations of the sound source and is dependent on distance from the source. The second is the displacement amplitude of the compression and rarefaction of the propagated pressure wave. At a distance of $\frac{\lambda}{2\pi}$ from the sound source (where λ is the wavelength), the two types of displacement are equal (van Bergeijk, 1964). The sound field from the source to the distance of $\frac{\lambda}{2\pi}$ away from it is called the near-field; beyond this distance it is called the far-field.

Formulae for calculating displacement amplitude (*d*) from pressure measurements in both the near-field and the far-field as used by Enger are:

$$d = \frac{p}{2\pi f \rho c}\left[1 + \left(\frac{\lambda}{2\pi r}\right)^2\right]^{1/2}$$

for the near-field, and $d = p/2\pi f \rho c$ for the far-field where d = displacement amplitude in centimetres, p = sound pressure in microbars, f = frequency in Hz, ρc = acoustic radiation resistance of water in grams per centimetre^2 per second, and r = distance from source in centimetres.

In the present study, thresholds were determined in the near-field at all frequencies except 400 Hz. Displacement amplitudes in Å were calculated for all frequencies using the appropriate of the above formulae (Table I, Fig. 6).

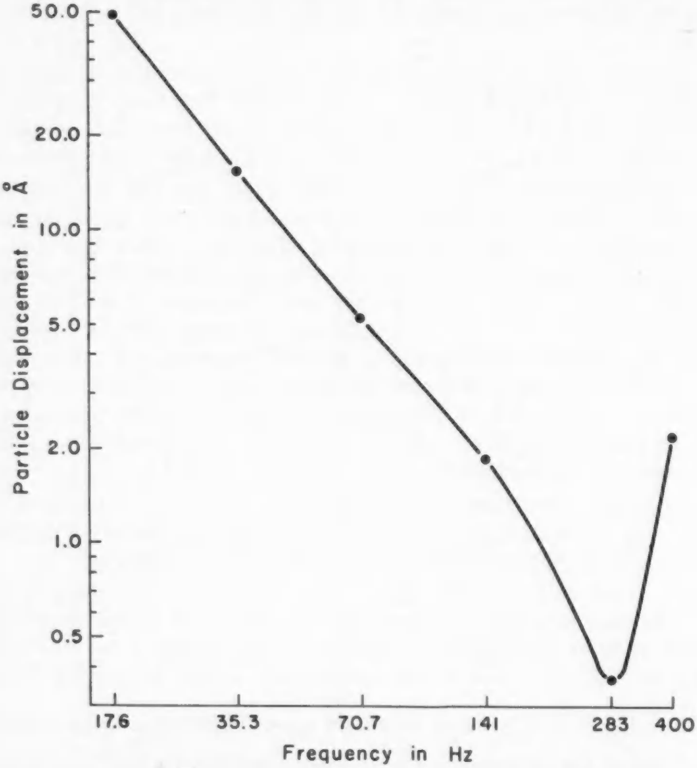


FIG. 6. Calculated particle displacement amplitude at threshold of 10 cod.

The particle displacement at threshold levels of cod for frequencies 17.6 to 400 Hz ranged from 49.36 Å to .37 Å. Interpolation on Fig. 6 shows displacement thresholds at frequencies 50, 100, and 200 Hz to be 8.7, 3.2, and .9 Å. The displacement at 400 Hz is 2.23 Å. These displacements are about 9, 16, 22, and 450 times as large respectively as those reported for goldfish at the same frequencies (Enger, 1966). The lower sensitivity of cod must undoubtedly be attributed, at least in part, to their lack of specialisation for auditory perception. It is also interesting to note that the difference in auditory sensitivity between goldfish and cod becomes increasingly greater as frequency rises.

The thresholds presented here were determined in the presence of background noise, and are therefore not absolute thresholds. The effect of background noise on thresholds, however, did not become obvious until background noise levels were converted from octave band levels to 1 Hz band levels (Fig. 2). Upon conversion, it could be seen that the threshold curve follows approximately the background noise levels over the frequency range of 17.6–283 Hz. Over this range, thresholds are an average of 28.7 db above noise, with a 95% fiducial interval of ±6.6 db. The threshold at 400 Hz on the other hand does not fit the trend. It is 64.7 db above background noise, and is suspected of being uninfluenced by noise. It could be regarded as an absolute threshold.

It would be desirable to determine the absolute threshold at other frequencies as well as at 400 Hz, but to make an experimental tank quiet enough at these low frequencies is extremely difficult. From the data presented, however, one can predict that absolute thresholds at frequencies 17.6, 35.3, 70.7, and 141 Hz would be much lower than the ones measured.

ACKNOWLEDGMENTS

I would like to thank Dr F. W. H. Beamish for his help, enthusiasm, and advice in initiating this study. I would also like to thank Dr J. L. Hart, Director of the St. Andrews Station, for allowing me to use the material for a thesis at McGill University. I wish to express special gratitude to Dr V. M. Pasztor and to Dr F. D. McCracken for their help in organizing the material. For technical assistance during the early stages of this project I am grateful to the Naval Research Establishment at Dartmouth, N.S.

REFERENCES

Albers, V. M. 1965. Underwater acoustics handbook — II. The Pennsylvania State University Press, University Park, Pennsylvania. 310 p.

Bergeijk, W. A. van. 1964. Directional and nondirectional hearing in fish. *In* W. N. Tavolga [ed.] Marine bio-acoustics. Pergamon Press, Oxford. p. 281–299.

Enger, S. 1966. Acoustic threshold in goldfish and its relation to the sound source distance. Comp. Biochem. Physiol., **18**: 859–868.

Moore, H. L., and H. W. Newman. 1956. Effects of sound waves on young salmon. U.S. Fish Wildlife Serv., Spec. Sci. Rept., Fish., No. 172.

Stevens, S. S. 1961. Is there a quantal threshold? *In* W. A. Rosenblith [ed.] Sensory communication. Wiley, New York. p. 806–813.

Tavolga, W. N., and J. Wodinsky. 1963. Auditory capacities in fishes. Pure tone thresholds in nine species of marine teleosts. Bull. Am. Museum Nat. Hist., **126**: 177–240.
1965. Auditory capacities in fishes. Threshold variability in the blue-striped grunt (*Haemulon sciurus*). Animal Behaviour, **13**: 301–311.

Wenz, G. M. 1964. Curious noises and the sonic environment in the ocean. *In* W. N. Tavolga [ed.] Marine bio-acoustics. Pergamon Press, Oxford. p. 101–119.

Wisby, W. J., J. D. Richard, D. R. Nelson, and S. H. Gruber. 1964. Sound perception in elasmobranchs. *In* W. N. Tavolga [ed.] Marine bio-acoustics. Pergamon Press, Oxford. p. 255–268.

Orientation of Pink Salmon (*Oncorhynchus gorbuscha*) During Early Marine Migration from Bella Coola River System[1]

By M. C. Healey[2]

Fisheries Research Board of Canada
Biological Station, Nanaimo, B.C.

ABSTRACT

During May and June 1966, the migration of pink salmon fry from the Bella Coola River was studied in Burke Channel, British Columbia. The movement of pink fry down Burke Channel was saltatory. Short periods of active migration were interspersed with longer periods when the fry did not migrate and accumulated in bays. Fry were sampled from these accumulations and their ability to orient using celestial cues was examined. During the early morning, fry tended to prefer directions at right angles to their direction of migration, but at other times of the day preferred the direction of migration. The preference for the direction of migration was strongest at midday. Fry were better oriented on clear days than on cloudy days. These data indicate that fry may use celestial cues to find directions during their oceanic migrations.

INTRODUCTION

A great deal of attention has been directed toward the freshwater migrations of juvenile Pacific salmon (genus *Oncorhynchus*) (Hoar, 1958; McDonald, 1960), and toward the oceanic and freshwater migrations of adult salmon (Ellis, 1962; Hasler and Wisby, 1951; Vernon et al., 1964). On the other hand, practically no attention has been paid to the early oceanic migrations of young salmon from the river mouths to the Pacific nursery area. These migrations are important because they occur during a period of heavy mortality in salmon stocks (Parker, 1962). The longer the young fish spend in the coastal environment, the greater is their mortality. A knowledge of the mechanism of migration is necessary before stocks can be manipulated to reduce this mortality. Also from the standpoint of management, the early migrations may provide clues to the routes and methods of navigation used by the adults on their return. And the outward migrations occur while the fish are of a more manageable size for experimentation than the returning adults.

The movement of pink salmon fry (*Oncorhynchus gorbuscha*) out of the Bella Coola River and down Burke Channel provides a unique system in which to study the early marine migrations of Pacific salmon. The Bella Coola stock remains relatively uncontaminated for much of its journey down North Bentinck Arm and Burke Channel (Fig. 1). Also the migration occurs in an enclosed

---

[1] Received for publication March 22, 1967.

[2] Present address: University of Aberdeen, Culterty Field Station, Newburgh, Aberdeenshire, Scotland.

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

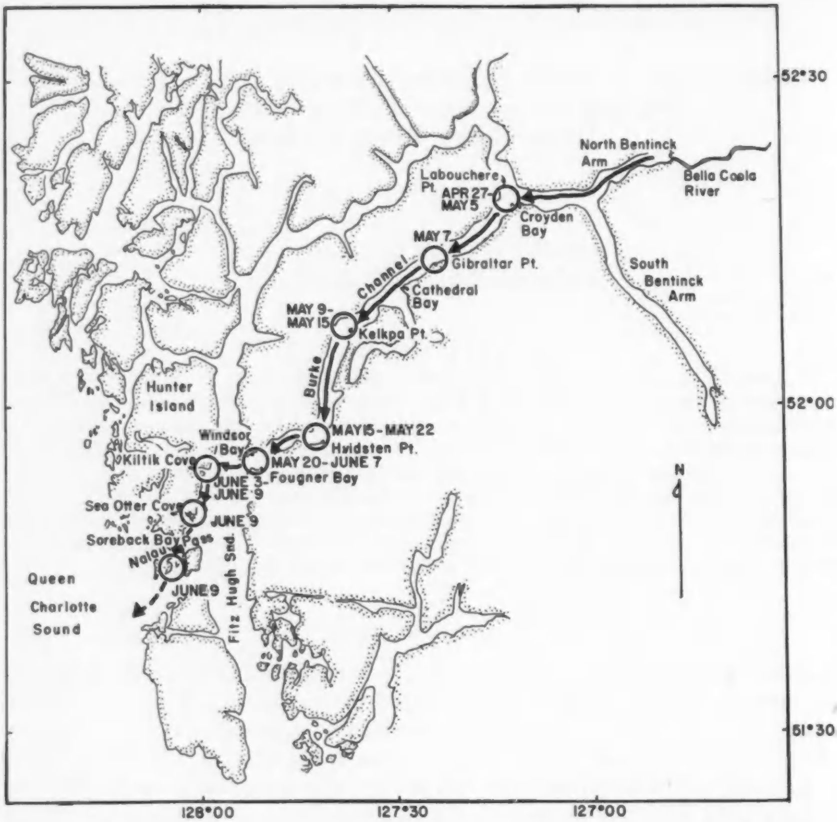

52°30
North Bentinck Arm
Bella Coola River
Labouchere Pt.
APR 27-MAY 5
Croyden Bay
MAY 7
Gibraltar Pt.
South Bentinck Arm
Channel
Cathedral Bay
MAY 9-MAY 15
Kelkpa Pt.
Burke
Hunter Island
52°00
MAY 15-MAY 22
Hvidsten Pt.
Windsor Bay
Kiltik Cove
MAY 20-JUNE 7
Fougner Bay
JUNE 3-JUNE 9
N
Sea Otter Cove
JUNE 9
Soreback Bay
Nalau Pass
Fitz Hugh Snd.
Queen Charlotte Sound
JUNE 9
51°30
128°00
127°30
127°00

FIG. 1. Bella Coola area, British Columbia, showing the migration route of the Bella Coola pink fry (arrows) and major points of accumulation (circles with dates alongside).

waterway so that the fish are quite easy to capture and observe during the first month and a half of their sea life. Consequently, detailed observations on the movements of pink fry in the Burke Channel system were begun in 1966. Since it is not possible to continue this study at the present time the following report has been prepared on the first summer's work. It should be emphasized that this study is still in the preliminary stages of development and all conclusions presented in this paper are tentative.

THE GENERAL PATTERN OF MIGRATION

Parker (1965) gives a general description of the migration of pink fry from the Bella Coola River to Nalau Pass on Hunter Island (Fig. 1) during 1962. The 1966 fry population was relatively small so that direct observations of migrating fry were time consuming and did little more than substantiate

Parker's earlier observations. Briefly the characteristics of the migration are as follows: pink fry leave the Bella Coola River in late April and spend about 30 days travelling from the mouth of the river to the mouth of Burke Channel. The movement down Burke Channel is not a continuous migration but a saltatory one. The fry may spend a day or 2 days actively migrating, and during this time may travel 20 miles or more down the channel. Then migration stops and the fish hold up for several days in quiet bays and backwaters. The fry are most easily observed during the periods when they are accumulated in bays, and at these times are concentrated close to shore. However, this shore-seeking tendency may not apply to the periods of active migration. In fact, the few times that active migration was actually observed, schools were seen moving well offshore.

The approximate timing of the 1966 migration and areas of accumulation are shown in Fig. 1. Considerable time was spent watching fry while they were accumulated in bays. The fry were always schooled, even at night when phosphorescence made them visible. In the larger bays the schools tended to mass along the shore. The fry fed actively at all states of the tide. Sometimes during the flooding tide small schools of fry moved along the shore to the entrance of the bay and fed in the tide turbulence there, but during the ebbing tide the schools moved back into the shelter of the bay. School movements in the bays were generally circular, and a given school sometimes stayed in the same area for hours. The schools moved close enough to the surface to dimple the water. Occasionally fish jumped completely out of the water. Schools that were actively migrating also moved close to the surface, but jumping was not observed.

At the mouth of Burke Channel the fry must overcome their attraction to the shore, because they move across the open waters of Fitzhugh Sound to Hunter Island. Once at Hunter Island, however, the fry resume their characteristic stop-go migration and accumulate in bays and back eddies once more.

CONTROLLING FACTORS IN MIGRATION

In spite of their apparently low migratory drive, pink fry do get from the mouth of the Bella Coola River to Hunter Island, a distance of well over 60 miles. Several factors could influence or control this migration.

One possible controlling factor is salinity. Baggerman (1960) and McInerney (1964) have shown that newly emerged pink fry have a definite preference for water more saline than their river waters. And as they get older the fry prefer greater and greater salinities. McInerney (1964) suggests that the fry may use salinity gradients to orient their migrations down coastal inlets.

A second possibility is that fry use tidal flow. They may allow themselves to be transported passively by the ebb, but utilize shore turbulence and back eddies to avoid being carried up channel by the flood. Creutzberg (1963) reports that eel elvers (***Anguila vulgaris***) use odour to distinguish between ebb and flood tide, and make use of the flood tide to move inshore. Pink salmon may move down Burke Channel in a similar manner.

A third possibility is that the fry follow food gradients to the mouth of Burke Channel. Pink salmon grow at a tremendous rate during their early sea life (LeBrasseur and Parker, 1964). The food requirements necessary to maintain their high growth rate may force the fry to move down Burke Channel.

Finally the fry may use celestial cues to orient toward the outlet. Groot (Johnson and Groot, 1963; Groot, 1965) has demonstrated the ability of migrating sockeye smolts (*O. nerka*) to use the sun as a direction-finding cue. It is reasonable to suppose that two such closely related species might use similar orientation mechanisms.

At present there is very little evidence to indicate which of these factors, or what combination of them, provides the best working hypothesis for a directing mechanism in the migration of pink fry. There are objections to all of them. Although average salinity measurements indicate increasing salinities toward the mouth of Burke Channel, salinity profiles are so subject to local conditions that they show very little consistency from day to day, or tide to tide. Furthermore, the bays and bights in which the fish accumulate often have streams flowing into them which lower the salinity of the surface waters. Passive drift with the current would seem to be ruled out, since fry schools were seen actively bucking an inflowing tide during one stage of their migration through Nalau Pass. There is no evidence for changes in food abundance related to periods of migration. A tremendous run of young salmon occurred in 1961, yet the timing of migration and the growth rate of the fry were similar to those in years of lesser abundance. Certainly an abundance of food is necessary to the fish, and food shortage may be a sufficient stimulus to migrate. But it is doubtful that food shortage is a necessary stimulus for migration or that food could act as a directing factor. The sun might act as a directional cue in migration. But because of the high, steep sides of the inlet the sun is directly visible for only a few hours each day. Groot (1965) found that sockeye smolts can orient well when the sun is below the horizon. In fact, sockeye migrate most actively at dusk. When the sun is below the horizon fish may orient using light patterns, or plane polarization in the sky (Dill, 1965). However, in Burke Channel the water surface is almost always rippled. Although ripples may make orientation easier when the sun is visible (Henderson, 1963), ripples almost certainly disrupt both light patterns caused by the sun and the polarization pattern of the sky.

The strongest single argument against salinity gradients, currents, and food gradients is that, though they could conceivably direct the fry in a closed waterway, they cannot direct them in the open ocean. This means that if the fry were following, say, salinity gradients, when they reached the mouth of Burke Channel, they would have to switch to some other mechanism in order to cross Fitzhugh Sound. In spite of difficulties in the sun compass hypothesis, the sun provides the most consistent stimulus to which the fry could orient. These considerations, combined with Groot's (1965) evidence for sun-orientation in sockeye, and the evidence of Hasler et al. (1958) for sun-orientation in other fishes, make sun-orientation a likely directing mechanism in pink fry migrations.

Therefore a program was organized in 1966 to study directional orientation of pink fry permitted only to see the sky. Three questions were asked during this study: (1) Do captive pink fry show a preference for any particular direction when they can only see the sky? (2) If there is a preferential direction is it constant or does it fluctuate diurnally? (3) Do overcast conditions affect the directional preference? The outcome of these experiments is described below.

ORIENTATION EXPERIMENTS

Materials and Methods

The apparatus used to study orientation (Fig. 2) was the same as that used by Groot (1965). A single pink fry was placed in each of the small circular tanks (30 cm diam × 30 cm high). The high opaque sides of these tanks effectively excluded all landmarks such as hills and trees. The fry were prevented from seeing out through the clear bottoms of the tanks by the heavy black plastic sheeting that covered the supporting frame. The tanks were filled with

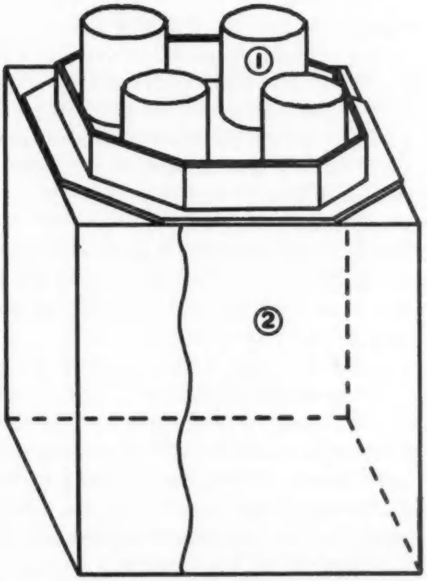


Fig. 2. The apparatus for orientations. 1, 30-cm diam × 30-cm high testing tank; 2, enclosed supporting frame.

seawater to a depth of 15 cm. This gave the fish a 90° angular view of the sky from the water surface at the centre of the tank.

Fry were given at least an hour to adjust to the tank before observations were begun. Observations were made on a single fry by the experimenter, who lay underneath the tank and looked up through the clear plastic bottom of the tank. To facilitate observations the bottoms of the tanks were ruled off into eight radial segments, each representing a compass direction. The observer recorded both the position of the fish (i.e., the wedge-shaped sector it was sitting above) and its direction of pointing. All changes of position were recorded but a pointing was scored only when the fish held position and pointed in one direction for 3 sec. If the fish held position and pointed for 6 sec two pointings were scored, and so on. The period of 3 sec was estimated by the observer by counting to three slowly.

Each fry was observed for 15 min; therefore, the maximum pointing score for a single test was 300. However, an active fry might score only a few pointings. Two to four tests were made on different fry each testing period, and there were up to six testing periods in a day. The same fry were generally used for all of a single day's testing. The fry were left in the experimental apparatus between testing periods. A constant supply of water was not available for cooling the tanks. Nevertheless air temperature was never very high and the tank water was changed frequently so that temperatures in the tanks seldom rose above 16 C. When consecutive tests were made on the same fry, a bias was introduced if the fry tended to orient to some mark on the inside of the tank. To avoid this bias each tank was rotated 0°, 90°, 180°, or 270° in a random order between tests.

Other behaviour noted and recorded was food catching, surface nipping, spitting, dashing, mumbling, and yawning. These acts are described for sockeye smolts by Groot (1965). They are identical in pink salmon.

A total of 88 tests of the type described above were performed on pink fry sampled from the wild migrating stock between May 2 and June 10. In addition, eight fish were saved from the early testing series and retested at various stages of the run. Most of the tests were performed between 11:00 AM and 7:00 PM, but data are available for four testing periods: early morning (6:00 AM – 10:00 AM), noon (10:00 AM – 2:00 PM), mid-afternoon (2:00 PM – 6:00 PM), and evening (6:00 PM – 10:00 PM). Several attempts were made to test fish after dark, but this proved impossible. Tests were performed during all types of weather except heavy rain.

Proper statistical tests for the data collected are difficult to find. Batschelet (1965) and Waterman (1963) give numerous tests applicable to data which are cyclic in nature, but none of these is suitable for my data. Groot (1965) used vector analysis (Krumbein, 1939; Durand and Greenwood, 1958) to analyse his data. For several reasons I feel that vector analysis is not suitable for the type of data I collected. First, although individual tests are independent of one another, the pointings within a single test are not. One of the assumptions underlying the vector analysis is that individual observations are independent.

The vector analysis gives unbiased estimates of mean pointing direction and variance when the pointings are symmetrically arrayed around the mean. Much of my data showed an asymmetric distribution. The test cannot be used on data with more than one mode, although modes in 180° opposite directions can be handled by using the second trignometric moment (Batschelet, 1965). However, this necessitates a subjective decision about bimodality, and when there are numerous borderline cases such decisions are dangerous. Groot appears to have used the test on data lumped from several tests. I believe this is a faulty procedure for two reasons. The number of pointings observed differs markedly between tests. When data are lumped fry which are strongly oriented but which give few pointings because they are restless in the tank may be swamped by fry which are disoriented but give many pointings. Or a fry well oriented in one direction but with few pointings may be masked by a fry well oriented in another direction but with a lot of pointings. The problem of masking one orientation with another in this way is doubly serious since, as Groot points out, restlessness in the tank may be indicative of migratory drive. Hence, a restless fry with few pointings may give a better indication of migration orientation than a quiet fry with lots of pointing scores.

In order to avoid some of these difficulties the orientation data were treated in the following manner. First, each test was divided into pointing scores along the axis of migration and pointing scores at right angles to the axis of migration. The axis of migration was determined by the axis of the inlet. All the tests on fish from a particular point in the migration were treated as a unit. χ^2 values were calculated for those tests showing more pointings along the axis of migration than at right angles to the axis. All tests in which the χ^2 value indicated a probability of $P < 0.05$ were given a + score. The number of + scores has a binomial distribution and:

$$Z = \frac{n(+) - 0.05N}{\sqrt{0.05(0.95)N}}$$

where Z is the normal statistic; $n(+)$ is the number of + scores; and N is the total number of tests in the sample. Z indicates the probability of getting $n(+)$ scores by chance alone in a set on N observations. $P < 0.05$ when $Z > 1.36$. The actual choice of acceptance level for the original χ^2 tests is arbitrary since a greater probability level of acceptance merely increases the number of + scores expected by chance. However, the choice of $P < 0.05$ as an acceptance level does give some indication of the number of tests which actually do show orientation along the axis of the inlet.

This method of testing is not as sophisticated as the vector analysis used by Groot. It does not give a mean pointing direction or a variance, for example. But since it avoids the pitfalls of lumping tests, and some of the problems of dependent pointing scores, I feel it is a more realistic way of treating the data.

RESULTS

The first consideration is whether there is any overall relationship between the direction of fry migration and the direction of pointing in the tanks. During the first stage of their 1966 migration the fry moved down Burke Channel to Fougner Bay and Windsor Bay at its mouth. Their axis of migration at this stage was generally southwest. Then the fry moved across Fitzhugh Sound to Kiltik Cove on Hunter Island, a west-southwest direction. From Kiltik Cove the fry migrated south to Nalau Pass, then down Edward Channel to Queen Charlotte Sound. Allowing for the shift in migration direction from southwest to west-southwest at Fougner Bay, pointings along the axis of migration and across the axis can be compared. The lumped results from noon and afternoon tests at each sampling point are shown in Table I. Only noon and afternoon tests are compared since morning tests were not made on all samples. At every stage of the migration there were significantly more pointings along the axis of migration than at right angles to it.

TABLE I. Numbers of pointings (noon and afternoon) along the axis of migration and across the axis of migration at various stages of the 1966 pink fry migration.

Date	Origin of sample	No. of tests	Pointings along migration axis	Pointings across migration axis	χ^2	P
May 4–6	South of Labouchere Point	20	2537	1984	67.88	$<.001$
12	Kelkpa Point	8	1187	967	22.46	$<.01$
17	Hvidsten Point	8	1071	897	15.38	$<.05$
22	Fougner Bay	6	818	689	10.88	$<.10$
26–27	Fougner Bay	9	1211	894	47.46	$<.001$
29–30	Fougner Bay	12	1818	1376	61.16	$<.001$
June 10	Kiltik Cove	8	1235	875	61.42	$<.001$

The lumped data indicate that the fry have a definite preference for directions along the axis of migration. But before a more detailed analysis can be made any effects of time of day must be examined. Comparisons of pointings along the axis of migration and at right angles to it are shown in Table II for the four daily testing periods.

In the early morning the fry tend to prefer directions at right angles to the direction of migration. By noon, however, the fry prefer the migration direction. They continue to prefer the migration direction throughout the afternoon and evening, although the preference is very weak by evening. In terms of directional preference then, noon, afternoon, and evening data may be treated together, but morning data should be treated separately.

Sockeye, in contrast to pink fry, are most strongly oriented at dusk. Sockeye also migrate most actively at dawn and dusk. Although the number

TABLE II. Numbers of pointings along the axis of migration and across the axis of migration at different times of day.

Time of day	No. of tests	Pointings along migration axis	Pointings across migration axis	χ^2	P
Early morning (6–10 AM)	17	1553	1837	23.79	$<.10$
Noon (10 AM–2 PM)	24	3153	2218	162	$<.001$
Mid-afternoon (2 PM–6 PM)	18	2821	2134	95	$<.001$
Evening (6–10 PM)	29	3954	3520	25.2	$>.05$

of observations is small, pink fry were seen to migrate during midday. These differences in orientation behaviour, therefore, may reflect basic differences between sockeye and pink salmon in time of migration.

The next step in the analysis is to consider the behaviour of the fish in individual tests (Table III). χ^2 values were calculated for tests showing more pointings along the axis of migration. Two points may be made from Table III. First, out of a total of 71 afternoon and evening tests, 51, or 72%, show more pointings along the axis of migration than across. The χ^2 tests applied to lumped data in Table I gain weight from these figures, since it is obvious that the lumped results were not biased by a few well-oriented fish with high pointing scores. The binomial test, described earlier, was applied (Table IV) to the data from each sample of fry separately. As might be expected from the lumped data, a highly significant number of fish show a preference for the axis of migration.

Too few early morning tests were made to warrant subdivision into samples; however, the lumped data from morning tests show that the fry preferred directions at right angles to the direction of migration. Of the 17 tests done in early morning 11 show more pointings at right angles to the direction of migration and six of these were significant ($Z = 7.231$, $P < .001$).

The results of tests performed on fish caught at the start of the run and held alive in a tank on the research vessel until the end of the run are presented in Table V. The pelleted fry food fed to these fish was not a sufficient diet to keep them growing, and all were "pinheads" in a week or so. The generally poor condition of these fish makes the results of tests performed on them of dubious value. Only in the first series of tests, performed just after the fish were caught, do they show significantly more pointings along the axis of migration.

The afternoon data presented above indicate a preferred orientation along the axis of normal migration by the fry in the experimental apparatus. Orientation to landmarks such as shorelines and trees is ruled out since the fish

TABLE III. The results of individual tests on wild-caught pink fry during the 1966 migration.

Date	Origin of sample	Time of day	Pointings along axis	Pointings across axis	χ^2	P
May 4	South of Labouchere Point	AM 11:00	48	39	0.926	ns[a]
		11:30	300	0	300	$<.001$
		PM 1:00	94	192	–	–
		1:30	154	135	1.238	ns
		6:00	61	166	–	–
		6:30	168	91	22.9	$<.001$
		8:00	171	120	8.9	$<.01$
		8:30	172	127	8.5	$<.01$
May 5	"	AM 11:30	27	26	0.01	ns
		11:30	165	91	21.4	$<.001$
		PM 1:00	95	60	7.9	$<.01$
		1:30	165	73	29.4	$<.001$
		6:00	155	123	3.86	$<.05$
		6:30	132	144	–	–
		8:00	139	144	–	–
		8:30	121	161	–	–
May 6	"	1:00	97	63	7.22	$<.01$
		1:30	78	60	2.34	ns
		8:00	62	46	2.37	ns
		8:30	133	132	0.00	ns
May 12	Kelkpa Point	1:00	129	85	9.00	$<.01$
		1:15	104	192	–	–
		3:30	85	198	–	–
		3:45	258	39	161	$<.001$
		6:00	241	26	173	$<.001$
		6:15	70	160	–	–
		8:15	152	116	4.83	$<.05$
		8:30	138	152	–	–
May 17	Hvidsten Point	AM 11:30	71	134	–	–
		11:45	256	33	171	$<.001$
		PM 12:30	173	124	8.66	$<.01$
		12:45	114	157	–	–
		3:15	132	183	–	–
		3:55	187	112	19.1	$<.001$
		7:37	17	10	1.81	ns
		7:50	120	144	–	–
May 22	Fougner Bay	AM 11:30	130	112	1.34	ns
		11:45	127	95	4.61	$<.05$
		PM 2:00	151	104	8.66	$<.01$
		2:15	148	133	0.800	ns
		6:45	125	110	0.958	ns
		7:00	137	135	0.007	ns

(Continued)

TABLE III. The results of individual tests on wild-caught pink fry during the 1966 migration. — (*Concluded*)

Date	Origin of sample	Time of day	Pointings along axis	Pointings across axis	χ^2	*P*
May 26	Fougner Bay	PM 4:30	154	121	3.96	$<.05$
		4:45	152	126	2.43	ns
		6:20	156	70	32.7	$<.001$
		6:45	81	154	–	–
		7:00	164	54	61.12	$<.001$
May 27	"	1:15	140	136	0.030	ns
		1:30	20	22	–	–
		4:05	163	110	10.2	$<.01$
		4:20	181	123	11.0	$<.001$
May 29	"	AM 11:25	138	93	8.76	$<.01$
		11:40	300	0	300	$<.001$
		PM 2:50	126	139	–	–
		3:10	133	120	0.620	ns
		6:40	120	106	0.869	ns
		7:00	140	157	–	–
May 30	"	1:15	150	146	0.028	ns
		1:30	98	149	–	–
		4:10	199	90	41.1	$<.001$
		4:30	172	65	52.76	$<.001$
		6:30	150	139	0.419	ns
		6:45	97	162	–	–
June 10	Kiltik Cove	2:25	113	144	–	–
		2:45	106	116	–	–
		3:08	190	94	32.46	$<.001$
		3:27	181	117	13.74	$<.001$
		6:10	179	87	33.82	$<.001$
		6:25	153	108	7.44	$<.01$
		6:40	164	118	7.50	$<.01$
		7:00	149	91	14.02	$<.001$

[a]ns = not significant.

could not see them over the high sides of the testing tanks. The only visual cues available to the fish were celestial, i.e. the sun and the polarization pattern of the sky. If the fish make use of either of these cues in their migration, then overcast skies should cause confusion and disorientation. Pointing data from afternoon tests done during cloudy and clear weather were compared in a 2 × 2 contingency table. The results of this test should indicate whether cloud cover can affect the ability of the fry to orient:

Cloud cover, %	Pointings Along	Across	Σ	
< 50	4244	3248	7492	
> 50	4459	3649	8108	$\chi^2 = 4.399$
Σ	8703	6897	15600	

It is apparent from the contingency that the proportion of pointings along the axis of migration is higher on clear days (<50% cloud cover). And the differences between cloudy and clear days are significant ($P < .05$). Cloud cover also affects the early morning orientation of the fish. There is a much higher proportion of pointings at right angles to the axis of migration when the skies are clear ($\chi^2 = 51.54$, $P < .001$).

TABLE IV. "Z" values for each sample series of tests, calculated from Table III.

Date	Origin of sample	No. of tests	No. of tests, $p < .05$	Z	P
May 4–6	South of Labouchere Point	20	9	8.421	<.001
12	Kelkpa Point	8	4	5.901	<.001
17	Hvidsten Point	8	3	2.600	<.01
22	Fougner Bay	6	2	3.269	<.001
26–27	Fougner Bay	9	5	7.000	<.001
29–30	Fougner Bay	12	4	4.533	<.001
June 10	Kiltik Cove	8	6	9.180	<.001

TABLE V. The results of orientation tests performed on fish caught at the beginning of their migration and held until the end.

Date	Testing location	Pointings along axis	Pointings across axis	No. of tests	χ^2	P
May 5	Croyden Bay	995	822	8	16.68	<.05
13	Cathedral Bay	528	600	5	Across axis	
21	Fougner Bay	391	725	4	Across axis	
June 6	Soreback Bay	1033	1013	8	0.195	ns

One problem with the above methods of analysis is that pointings along the axis of migration include both orientation in the direction of migration and reverse orientation (i.e. facing in the direction 180° opposite to the migration direction). Reverse orientation in the small tanks presents a problem which is difficult to explain. Groot (1965) found higher proportions of reverse orientation in sockeye smolts early and late in the run when migratory drive was low, and when some barrier prevented swimming in the preferred direction. About 50% of the pink fry tested show reverse orientation. Both the factors that Groot suggests might influence reversal of orientation could be operative in pink fry. The small testing tanks certainly prevent swimming in a preferred direction. Also the fish tested were taken from accumulations in bays when migratory drive was low.

DISCUSSION

Two very general questions can be asked about any migration. The first question is: what stimulates the animals to migrate? Considering the saltatory type of migration shown by pink fry, they must be continually restimulated to migrate. What triggers the brief periods of migration is an open question. If solar orientation dominated the migration then clear weather might be expected to act as a stimulus. This does not appear to be the case. Considering the rapid growth rate of the fry, certain states of nutrition may be an important factor. The greater shoreward orientation shown by pink fry in the holding experiment may indicate a shore-seeking tendency in hungry fry that would carry them into bays and back eddies. However, much more work is necessary before an adequate hypothesis can be formulated.

The second question is: once the animals are stimulated to migrate, what directs their movements? The data collected in this study bear directly on this question. Before any generalizations can be made about directional preference in small tanks and normal migration, however, several assumptions must be satisfied. The first assumption is that the behaviour of the fish in the orientation apparatus is in some way related to migration. Most certainly the behaviour of a fry in the orientation tank is not normal. The tank is a closed system and quite small so that movement in any particular direction is severely restricted. The mere fact that direction of pointing rather than direction of swimming is used to indicate orientation bears this out. Yet the fact remains that fish in the tank do tend to point along the direction they would normally travel during migration. The simplest hypothesis at the moment is that these two phenomena are related. Some evidence that direction of pointing and direction of swimming are related is given in Appendix I. The second assumption has to do with the behaviour of a fish when it is alone and when it is with a group of other fish. During migration pink fry are schooled, yet only single fish were tested in the orientation apparatus. We must assume that factors influencing the orientation of a fry in a tank also influence its orientation in a school.

There are many unknowns with respect to schooling behaviour that we must discover as well, if correct interpretations of orientation data are to be made. For example, does a fish which is strongly oriented in a tank have a greater effect than one which is weakly oriented upon the movement of the school? Is schooling a "follow-the-leader" sort of mechanism or is the movement of the school a composite of the orientation tendencies of its members? Or is the school a "majority-rules" system such that if most fish tend to orient in one direction the rest just follow along and have very little influence upon the movement of the school? There may be social organization within a school that we are unaware of. If a school is a hierarchical system, then a very few fish may dominate its movement. There is very little evidence to help us decide which of these mechanisms is at work in the school. All of them may be present in different species.

A third problem related to interpretation is how well oriented a fish must be before the orientation is of any use in direction finding. In an enclosed waterway like Burke Channel a low level of orientation is probably alright since deviations would only bring the fry up against a shore which it could follow. But in the open ocean deviations of a few degrees may be sufficient to put the fish so far off course that it would become hopelessly confused when it reached shore. Certainly the accuracy of orientation observed in pink fry was not sufficient to direct them without reference to some fixed landmark. It is unlikely, however, that the full accuracy of orientation is realized in the small tanks. The restriction of directional movement may have caused searching behaviour which would add a lot of undirected pointings to the results, as well as increasing reverse orientation. Also, Kramer (1959) found that pigeons deprived of a view of the real horizon were poorly oriented. It is quite possible that the fry need a view of the natural horizon to accurately estimate the altitude and direction of the sun.

In spite of the many difficulties in interpreting the data on sun-orientation, a few cautious generalizations may be made. The fry showed their strongest orientation during noon and early afternoon, the periods when the sun was actually visible above the edge of the testing tank. Also fry were poorly oriented under overcast skies. Both these observations support an hypothesis of sun-orientation, and it seems almost certain that the fry are capable of using the sun to find directions. (A preliminary experiment to examine the ability of pink salmon to orient using a point light source is described in Appendix I.) Whether or not they actually do use sun-orientation during their migration is much less certain. However, the results are encouraging enough to warrent further examination of the problem along similar lines. Transplanting marked fry along the inlet either to speed up or retard their migration would provide information on the timing mechanism of the migration. Tests on the orientation of schools given a view of the sky only, such as those made by Groot (1965) might provide a more solid basis for the interpretation of orientation data from single fish.

ACKNOWLEDGMENTS

I should like to gratefully acknowledge the generous help and support of Dr R. R. Parker, without which this study would have been impossible. Cheerful technical assistance and samples of live fish were supplied by Messers R. C. Wilson, T. Cleugh, T. Leetma, and H. Neate. Drs R. R. Parker, J. R. Brett, and Mr Peter McCart read and criticised the text; however, these gentlemen cannot be blamed for any inaccuracies or faulty reasoning therein.

REFERENCES

BAGGERMAN, B. 1960. Salinity preference, thyroid activity, and the seaward migration of four species of Pacific salmon (*Oncorhynchus*). J. Fish. Res. Bd. Canada, **17**: 295–322.

BATSCHELET, E. 1965. Statistical tests for the analysis of problems in animal orientation and certain biological rhythms. A.I.B.S. Monograph. 57 p.

CREUTZBERG, F. 1963. The role of tidal streams in the navigation of migrating elvers, (*Anguila vulgaris* Turt.). Ergeb. Biol., **26**: 118–127.

DILL, P. A. 1965. Polarized light perception and orientation by yearling sockeye salmon (*Oncorhynchus nerka*). M.Sc. Thesis. University of British Columbia, Vancouver, B.C.

DURAND, D., AND J. A. GREENWOOD. 1958. Modification of the Rayleigh test for uniformity in analysis of two-dimensional orientation data. J. Geol., **66**: 229–238.

ELLIS, D. V. 1962. Preliminary studies on the visible migrations of adult salmon. J. Fish. Res. Bd. Canada, **19**: 137–148.

GROOT, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour, Suppl., **14**: 198 p.

HARTMAN, G. F. 1965. The role of behaviour in the ecology and interactions of underyearling coho salmon (*Oncorhynchus kisutch*) and Steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada, **22**: 1035–1081.

HASLER, A. D., R. M. HORRAL, W. J. WISBY, AND W. BRAEMER. 1958. Sun-orientation and homing in fishes. Limnol. Oceanog., **3**: 353–361.

HASLER, A. D., AND W. J. WISBY. 1951. Discrimination of stream odors by fishes and its relation to parent stream behaviour. Am. Naturalist, **85**: 223–238.

HENDERSON, H. F. 1963. Orientation of pelagic fishes: 1. Optical problems 2. Sonic tracking. Ph.D. Thesis. University of Wisconsin, Madison, Wisc.

HOAR, W. S. 1958. Evolution of migratory behaviour among juvenile salmon (*Oncorhynchus*). J. Fish. Res. Bd. Canada, **15**: 391–428.

JOHNSON, W. E., AND C. GROOT. 1963. Observations on the migration of young sockeye salmon (*Oncorhynchus nerka*) through a large complex lake system. Ibid., **20**: 919–938.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* and *S. trutta*). Rept. Inst. Freshwater Res., Drottningholm, **39**: 55–98.

KRAMER, G. 1959. Recent experiments in bird orientation. Ibis, **101**: 399–416.

KRUMBEIN, W. C. 1939. Preferred orientation of pebbles in sedimentary deposits. J. Geol., **47**: 673–706.

LEBRASSEUR, R. J., AND R. R. PARKER. 1964. Growth rate of central British Columbia pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Bd. Canada, **21**: 1101–1128.

MCDONALD, J. 1960. The behaviour of Pacific salmon fry during their downstream migration to freshwater and saltwater nursery areas. Ibid., **17**: 665–676.

MCINERNEY, J. E. 1964. Salinity preference: an orientation mechanism in salmon migration. Ibid., **21**: 995–1018.

PARKER, R. R. 1962. A concept of the dynamics of pink salmon populations. University of British Columbia. Institute of Fisheries, H. R. McMillan lectures in fisheries, Symposium on pink salmon, 1960. p. 203–211.

1965. Estimation of sea mortality rates for the 1961 brood year pink salmon of the Bella Coola area, British Columbia. J. Fish. Res. Bd. Canada, **22**: 1523–1554.

VERNON, E. H., A. S. HOURSTON, AND G. A. HOLLAND. 1964. The migration and exploitation of pink salmon runs in and adjacent to the Fraser River convention area in 1959. Intern. Pacific Salmon Fish. Comm. Bull. No. 15. 296 p.

WATERMAN, T. H. 1963. The analysis of spatial orientation. Ergeb. Biol., **26**: 98–117.

APPENDIX I

A series of conditioning experiments was planned to explore the ability of pink fry to orient by means of a point light source. In these experiments fry were to be trained to swim at different angles to a point light source. The series of experiments could not be completed. However, preliminary results from experiments in which fry were trained to swim toward the light support the hypothesis that fry are able to orient by means of a point light source. The results of these experiments are presented below.

MATERIALS AND METHODS

The experimental apparatus consisted of an octagonal plastic tank 1 m diam and 15 cm deep. This tank was placed in a darkened room and surrounded by a black plastic curtain. Four feeding tubes led through the curtain into the tank at alternating sides of the octagon. The tank was filled to a depth of 10 cm with seawater. Fresh seawater was continuously circulated into the tank through a single inlet on the side, and drained through a central drain. The tank was lighted by a 150-w frosted light bulb hung 1 m above the surface of the water. This light could be positioned above any of the four feeding tubes (Fig. 3). The light was controlled by a photoelectric cell that turned the light on at dawn and off at dusk, thus keeping daylength in the tank about normal.

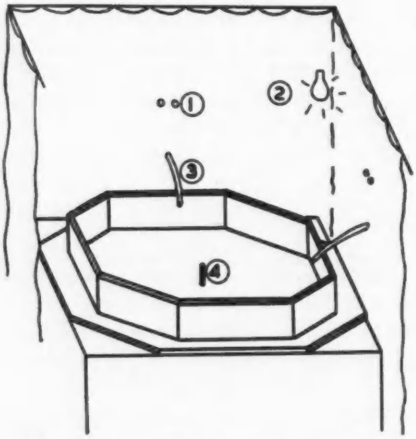


FIG. 3. The apparatus for conditioning pink fry. 1, peep holes in curtain; 2, movable light; 3, feeding tube; 4, octogonal testing tank.

Water was left circulating in the tank for 1 day before fish were introduced. Eight underyearling pink fry were introduced into the tank and allowed 1 day to adjust to the apparatus before experiments were begun.

One trial was run approximately every hour beginning at 8:00 AM the day after the fish were introduced. A trial consisted of first ringing a door buzzer that was taped to the side of the tank for 3 sec. A 3-sec pause followed the buzzer. Then a small amount of food was introduced through the food tube directly beneath the light. The food used was a composite of marine plankton (mostly euphasids) captured in surface tows in Georgia Strait. The fry obviously liked this food, but only a small amount was given at each trial so that the fish were always hungry and competition was keen.

The objective, of course, was to get the fish to swim toward the light in response to the buzzer and before the food was introduced. To prevent orientation to landmarks or water currents in the tank, the light was positioned above a new food tube, selected at random, after each test. A response was scored when a fish turned and swam toward the food tube at the sound of the buzzer and before food was introduced. Each fish that responded in this way scored 1, so that a maximum response scored 8, and no response scored 0.

Observations were made by the experimenter, who looked into the tank through eye level slits in the curtain.

RESULTS

Three experiments were attempted in which pink fry were expected to learn to swim toward the light source. Wild-caught fry were used for one experiment, and hatchery-reared fry for two. The hatchery fry were in poor condition, and most of them died soon after they were introduced into the conditioning tank. The results presented, therefore, refer only to the experiment with wild-caught fish, except where noted.

The development of the learned response in the fry is summarized in Table VI. Dill (1965) found that the initial response to light as a conditioned stimulus occurred after about 15 trials in sockeye salmon. Pink fry appear to learn equally rapidly. Dill's experiments showed that the response of the sockeye rose to a plateau between 30 and 50 trials. The response of the pink fry tested, however, did not reach a plateau. Their response to the buzzer followed a diurnal cycle, with little or no response at 8:00 AM and 9:00 AM, a peak response (~65%) by 11:00 AM, less response in the early afternoon, and a peak response again at 3:00 or 4:00 PM (Pacific Standard times) (Fig 4).

TABLE VI. Development of the learned response in pink salmon.

Trial No.	Response
1–5	No obvious response to buzzer
6	First aggressive encounter noted
7–8	No obvious response to buzzer, but aggression observed before each trial
9	Orientation toward feeding tube beneath light noted
10–14	Strengthened orientation response; aggression continues
15	First swimming response to buzzer
16–45	Fluctuating swimming response to buzzer, following diurnal pattern in Fig. 4; aggression continues; two fish jumped out of tank between 22nd and 32nd trials.

When they were first put into the tank the fry were very restless, but they soon settled down and either held position in the tank or swam slowly around. After about the 10th trial I noticed that the fish that were holding position were oriented toward the light. This orientation was not related to the particular direction of the light or water currents in the tank, or the position of the observer. Orientation toward the light appears to be a preliminary step in learning the swimming response.

Shortly before the fish learned to orient towards the light they began to show aggression toward one another. Pink salmon are generally considered to be non-aggressive, and Hoar (1958) wrote that aggression had never been observed between young pink salmon. Nevertheless, considerable aggression was seen among the pink fry used in these experiments. Only chases and nips were observed, however, not the lateral display described by Kalleberg (1958) and Hartman (1965) for other salmonids. In the experiments with hatchery fry an attempt was made to define

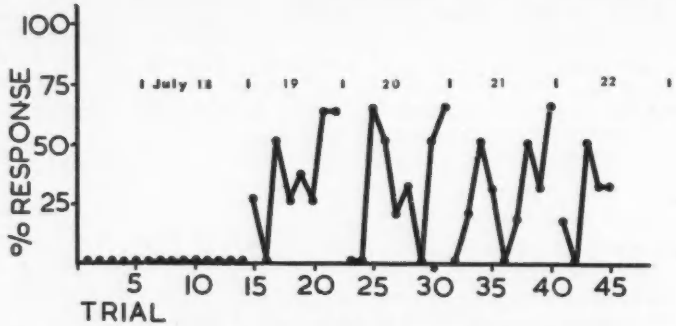


FIG. 4. The response to the conditioned stimulus showing a diurnal pattern after the 15th trial.

the social relationships within the tank. No stable hierarchy was formed, although the results may have been biased by the poor condition of the fry.

DISCUSSION

Little can be concluded from this experiment about the ability of pink fry to orient using a light source. Apparently the fry can react to a light and swim toward it. However, a much more critical test would be to train the fry to swim at an angle to the light. Such orientation is much more difficult since it requires more than just a simple phototactic response. Experiments of this type were planned but could not be carried out.

The diurnal pattern of response observed in the experiments may reflect some basic physiological rhythm in pink fry. However, the pattern may also be an artifact of small numbers. More experiments are necessary before it can be said that there is in fact a diurnal pattern of response.

The orientation response in these experiments also has bearing on sun-orientation in pink fry. In the conditioning experiments the direction of orientation of the fry was directly related to the direction in which they eventually swam. This point was assumed but not demonstrated in the tests on sun-orientation in migrating fry.

Muscle Weight Relationship to Serum Proteins, Hemocytes, and Hepatopancreas in the Lobster, *Homarus americanus*[1]

BY JAMES E. STEWART, JOHN W. CORNICK, DIANE M. FOLEY, M. F. LI, AND C. M. BISHOP

Fisheries Research Board of Canada
Halifax Laboratory, Halifax, N.S.

ABSTRACT

Total serum protein values, hemocyte numbers, and muscle weights were determined for 216 intermolt lobsters immediately after their capture, and for 230 others held captive under a variety of dietary and environmental conditions. Average muscle values ranged from approximately 13% to the more normal 20–25% of the live animals' weight, depending upon experimental conditions. The total serum protein up to a level of 55 mg/ml was shown to be a reliable indicator of muscle weights, although the relationship was not identical for all lobster groups. It appeared to be modified chiefly by the areas from which the different groups were taken. Diet was more important than the temperatures (5 to 14 C) in affecting changes in muscle and serum protein values. Starvation caused a greater reduction (50 to 70%) in the size of the hepatopancreas than in the muscle. Histological examination of the hepatopancreatic tissue showed that the lipid content was markedly reduced upon starvation and that a degeneration of this organ was apparent for lobsters fed a beef liver and herring diet. Measurement of serum proteins would appear to be a useful technique in experiments on lobster nutrition and have value, within specified limits, for assessing the physiological condition of wild lobsters.

INTRODUCTION

THE EXOSKELETON OF crustaceans prevents a visual assessment of the living animal's physiological condition, consequently we have been searching for an nondestructive method. Stewart et al. (1967) showed that changes in lobster (*Homarus americanus* Milne Edwards) hemocyte numbers and hemolymph protein levels are directly related to changes in the animals' diet, and we suggested that these measurements could be employed in nutritional experiments as indices of the efficiency of the diet. This report describes experiments designed to test this hypothesis. Accordingly, total serum protein values, hemocyte numbers, and muscle weights were determined for lobsters immediately after their capture and for others held captive under a variety of dietary and environmental conditions. The results confirm the original hypothesis by showing that serum protein values correlate well with the muscle values.

MATERIALS AND METHODS

LOBSTERS

Healthy, vigorous lobsters (*Homarus americanus*) of both sexes captured in the Nova Scotian littoral (Fig. 1, Table I) were used throughout the study.

---

[1]Received for publication August 14, 1967.

J. FISH. RES. BD. CANADA, 24(11), 1967.
Printed in Canada.

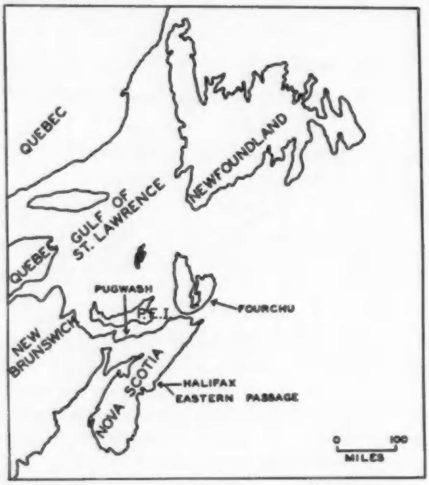


FIG. 1. Location of capture areas.

The lobsters' chelae were immobilized with rubber bands immediately after the animals' capture (Thomas, 1958; Wilder and McLeese, 1961), the standard practice in all our experiments. Measurements were made on 216 "wild" lobsters within 2 days of their capture and on 192 "captive" lobsters from Fourchu, N.S., and 38 others from Pugwash, N.S., after they had been held for extensive periods under a variety of conditions. The 192 Fourchu male lobsters (groups 9 through 16, Fig. 1, Table I) represented approximately half of a larger group of males (370) kept under the same conditions. A small percentage of these lobsters underwent ecdysis; these data are being reported separately. All the data reported here refer only to animals which showed no overt signs of molting.

EXPERIMENTAL CONDITIONS

The continuous flow seawater aquarium has been described previously (Stewart and Power, 1963). The tanks of recirculated, filtered seawater maintained at 14 C, the tanks supplied with free flowing seawater at ambient temperatures, the individual plastic shelters, the ratio of animals to space and volume, and the feeding schedules of beef liver and sardine herring were identical to those described previously (Stewart et al., 1967).

The different conditions to which the lobsters were subjected in this study are summarized in Table I and Fig. 2.

SERUM PROTEINS

Protein concentrations were determined for lobster serum (Lauffer and Swaby, 1955) by a modified biuret method (Layne, 1957), with bovine serum

TABLE I. Experimental conditions.

Group No.	Area of capture	Date of capture	No. of lobsters	Sex	Temp (*C*)	Food	Duration of captivity (*days*)	Maximum illumination (*lumens/ft*^{2})	Avg live wt (*g*)
1	Pugwash	September	31	M	Ambient	None	<2	N.A.[a]	544
2	"	"	29	F	"	"	<2	"	519
3	Eastern Passage	December	35	M	"	"	<2	"	506
4	" "	"	35	F	"	"	<2	"	522
5	" "	March	18	M	"	"	<2	"	555
6	" "	"	17	F	"	"	<2	"	550
7	Fourchu	July	25	M	"	"	<2	"	578
8	"	"	26	F	"	"	<2	"	511
9	"	"	20	M	"	H/B[b]	140	None	608
10	"	"	16	M	"	"	140	8	567
11	"	"	25	M	"	"	140	24	634
12	"	"	28	M	"	"	140	40	545
13	"	"	24	M	"	None	140	None	567
14	"	"	24	M	"	"	140	8	585
15	"	"	29	M	"	"	140	24	584
16	"	"	26	M	"	"	140	40	554
17	Pugwash	October	19	10 M, 9 F	14	H[b]	149 T[c]	N.A.	344
18	"	"	19	9 M, 10 F	14	None	149 T	"	316

[a] N.A. — not applicable — normal laboratory lighting.
[b] H = herring; B = beef liver; food in excess.
[c] T: held for initial 76 days at ambient temperatures; remaining time at 14 C.

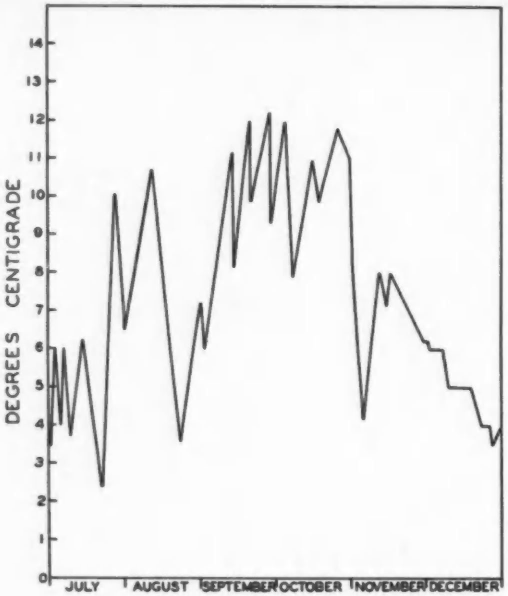


FIG. 2. Extreme values of ambient seawater temperatures in the aquarium during the course of the experiments.

albumin (Pro Sol, Standard Scientific Supply Corporation, New York, N.Y.) as the standard. The total serum proteins only were measured, since the increase or decrease in total plasma proteins has been shown to be a result of similar changes in all the protein components (Stewart et al., 1967).

HEMOCYTES

Lobsters hemocytes were counted, using a Model B Coulter Counter, by the method described previously (Stewart et al., 1967).

MUSCLE WEIGHT

Live lobsters were removed from seawater, dried rapidly with absorbent paper, and weighed prior to the removal of hemolymph samples for hemocyte and protein determinations. The lobsters then were boiled for 15 min in seawater to shrink the muscle away from the shell. The lobsters were removed from the boiling seawater and allowed to cool to room temperature. The tail was removed from the body at the carapace taking with it that part of the muscle which extends into the carapace and comes away easily with the tail. Both large claws or chelae were removed from the carapace of each lobster at the basipodite. The muscle was removed from the claws and tail and all extraneous material such as coagulated hemolymph protein, ovarian or hepatopancreatic matter was rinsed off, the endoskeletal elements were removed, excess moisture was drained, and the muscle was weighed.

ILLUMINATION OF LOBSTER TANKS

The lighting arrangement described by Stewart (1963) was used to provide a repetitive 24-hr program. The illumination program time (14 hr) was based on the hours of total daylight for this geographic position for August and September. The program allowed 1 hr for the gradual change from total darkness to maximum light intensity and 1 hr for the gradual change from maximum intensity to total darkness. The intensities were chosen as an approximation of the light intensities expected at approximately 20-m depth in coastal waters (Klugh, 1927; Kimball, 1928). The maximum illumination reaching the water surface was 0, 8, 24, and 40 lumens per ft^2 for 0-, 25-, 60-, and 100-w incandescent bulbs respectively. A Weston Illumination Meter Model 756 equipped with a Viscor filter (Weston Instruments and Electronics Division of Daystrom Inc., Newark, N.J.) was used to measure the light intensities.

HEPATOPANCREAS

The percentage of the lobsters' live weight attributable to the hepatopancreas was determined for wild and captive (both fed and starved) lobsters. The individual lobster was weighed; the hepatopancreas was removed, drained, and weighed. The remainder of the lobster was exposed to the boiling seawater and the amount of muscle was determined as before.

The excised hepatopancreatic tissue was fixed in 10% formalin neutralized with calcium carbonate, frozen, and then sectioned. Fixed frozen sections were taken from a location slightly posterior to the opening into the midgut. These sections were treated with albumin to overcome the difficulty experienced in keeping them on the slides. The sections were stained with Sudan Black in propylene glycol for lipids, Alcian Blue for acidic carbohydrates and by Best's method for glycogen (Humason, 1962).

STATISTICAL ANALYSIS

The calculation of values for the standard deviation, standard error of estimate, and correlation coefficients followed the procedures outlined by Goulden (1952). The F distributions for the ratios of the variances were calculated according to Dixon and Massey (1951).

RESULTS

The correlation coefficients (Table II) for the relationship between the percentage of muscle and serum proteins are highly significant except for the group fed on beef liver and herring. Correlation coefficients between hemocyte and muscle values are more variable; the coefficients for the two groups which were fed are not significant whereas those for the starved animals are.

TABLE II. Captive lobsters: hemolymph, muscle values, and their relationship.

Group No.	No. of lobsters	Sex	Temp (*C*)	Food	Duration of captivity (*days*)	Avg live wt (*g*)	Avg muscle % of live wt +SE[a]	Avg serum protein (*mg/ml*) +SE	Avg hemocytes/ $mm^3 \times 10^4$ +SE	Correlation coefficients: Serum protein vs. muscle content	Correlation coefficients: Hemocytes vs. muscle content
9–12	89	M	Ambient	H/B	140	589	24.3±0.25	62.9±1.42	2.96±0.06	0.299	−0.062
13–16	103	M	Ambient	None	140	573	17.7±0.23	29.2±1.14	1.87±0.06	0.759	0.625
17	19	M +F	14	H	149[b]	344	21.6±0.5	41.6±2.12	2.64±0.16	0.776	0.323
18	19	M +F	14	None	149[b]	316	13.2±0.79	15.6±2.81	0.78±0.13	0.924	0.848

[a] Standard error of estimate.

[b] Held for initial 76 days at ambient temperatures; remaining time at 14 C.

Changes in the total muscle are not confined to disproportionate changes in any one of the major body components. The data in Table III demonstrate that regardless of the treatment the distribution of muscle in the various parts of lobsters of the same general size remains constant. The smaller lobsters (groups 17 and 18) have disproportionately smaller claws than the larger lobsters and consequently have less of their total muscle in the claws and more in the tail. This is consistent with the changes in the lobster's proportions which occur with increasing size (Herrick, 1911).

The numbers of lobsters used for the examination of hepatopancreatic tissue (Table IV) were not considered sufficient for a statistical analysis but they do demonstrate that the general decline in muscle weight is accompanied by a similar decline in the hepatopancreas.

The hepatopancreatic tissue from the lobsters on the beef liver and herring diet floated when placed in the fixative whereas the tissue (3.4% of the live body weight) from only one of the starved lobsters floated. The rest sank as did the tissue from all of the wild lobsters examined histologically (five males).

The histological sections (Fig. 3) show that the lipid content of the hepatopancreas of the starved lobsters is greatly reduced. Little or no lipid material was apparent in the hepatopancreas of the two starved lobsters with the least amount of this tissue (1.6 and 1.8% of their live body weight respectively). The tissue from the two starved lobsters with the intermediate weights of hepatopancreatic tissue (2.8 and 3.4% of their live body weight) contained considerably less lipid than did tissue from the captive fed or wild lobsters. The sections from the starved lobster with the greatest amount of hepatopancreatic tissue (3.6% of the live body weight) was indistinguishable from the sections taken from the lobsters on the beef liver and herring diet. The sections from the captive fed lobsters showed diffuse staining whereas the sections from the wild lobsters' hepatopancreatic tissue showed the lipid to be in discrete droplets. The other histological tests failed to demonstrate glycogen or acidic carbohydrates in the hepatopancreatic tissue from any of the groups.

The lack of a response to the different light regimes is illustrated by the data in Table V. The F distributions for the ratios of the variances were calculated and confirm that light alone was not a significant factor in altering the muscle weight of the lobsters; food was highly significant at the 5% level. The interaction of light with food was not significant. The correlation coefficients (Table V) for the starved groups are all significant at the 1% level whereas only the protein:muscle coefficients for groups 11 and 12 are significant at the 5 and 1% levels respectively.

The values for serum proteins, hemocytes, and the muscle content of the wild lobsters are presented in Table VI together with the correlation coefficients derived from these data. The coefficients for the relationship between the hemocyte numbers and the muscle values for groups 5, 6, 7, and 8 are not significant; for group 4 it is significant only at the 5% level whereas the coefficients for groups 1, 2, and 3 are significant at the 1% level. The relationships

TABLE III. Percentage distribution of total muscle between chelae and tail for all lobsters.

Group No.	No. of lobsters	Sex	Temp (*C*)	Food	Duration of captivity (*days*)	Maximum illumination (*lumens/ft²*)	Avg carapace length (*mm*)	Avg live wt (*g*)	Muscle % of live wt	Muscle distribution (%)		
										Pincer	Crusher	Tail
1 and 2	60	M F	N.A.	N.A.	2	N.A.	89	527	22.1	19.9	30.1	50.0
3 and 4	70	M F	"	"	2	"	88	514	21.9	21.0	26.2	53.0
5 and 6	35	M F	"	"	2	"	91	552	20.8	21.9	27.7	51.4
7 and 8	51	M F	"	"	2	"	88	544	22.9	20.4	29.3	50.3
9	20	M	Ambient	H/B	140	None	92	608	25.4	20.4	30.7	48.9
10	16	M	"	"	140	8	89	567	24.3	22.7	28.5	48.7
11	25	M	"	"	140	24	92	633	23.6	21.6	32.3	46.3
12	28	M	"	"	140	40	88	545	24.2	22.1	30.1	48.1
13	24	M	Ambient	Starved	140	None	89	567	18.1	21.5	27.7	50.7
14	24	M	"	"	140	8	90	585	18.2	20.8	29.4	49.8
15	29	M	"	"	140	24	92	584	17.1	20.8	28.4	50.8
16	26	M	"	"	140	40	88	554	17.8	20.9	28.9	50.3
17	19	M F	14	H	149	N.A.	Approx. 66	344	21.6	18.4	24.0	57.6
18	19	M F	14	Starved	149	"	Approx. 66	316	13.2	17.7	22.9	60.4

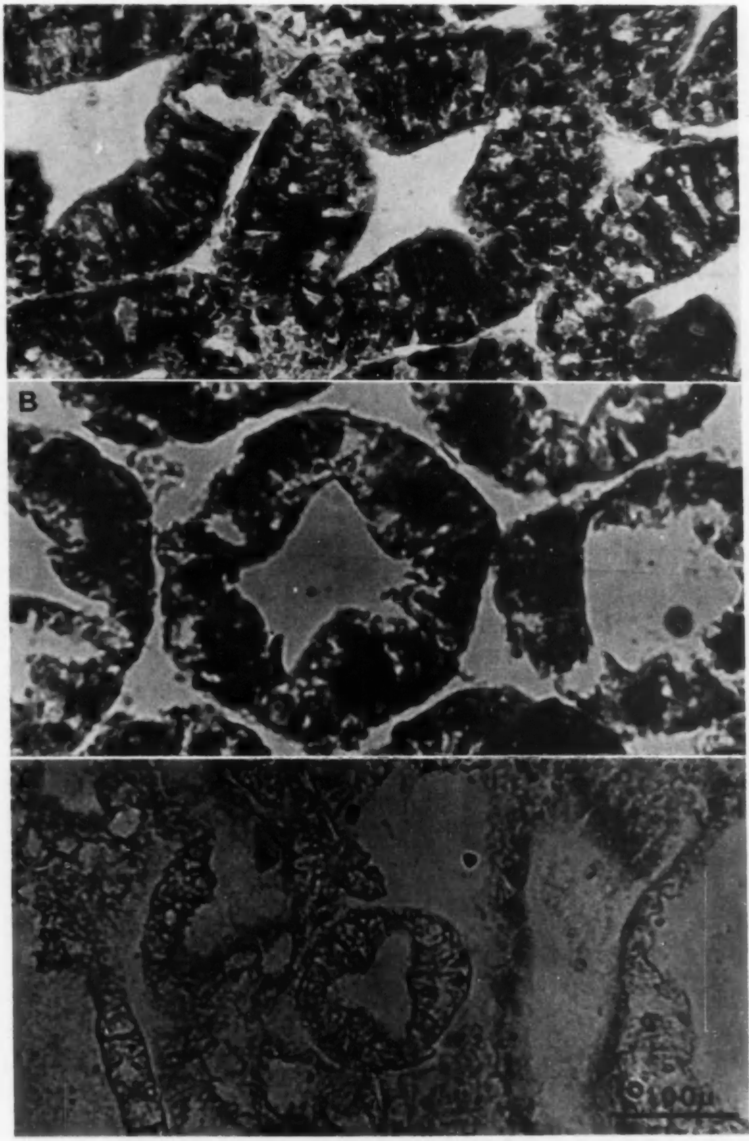


FIG. 3. Lobster hepatopancreatic sections stained with Sudan Black; A, wild lobster; B, captive lobster on beef liver and herring diet; C, starved lobster.

TABLE IV. Hepatopancreas as percentage of lobsters' live weight.

Group No.	No. of lobsters	Sex	Temp (*C*)	Food	Duration of captivity (*days*)	Avg live wt (*g*)	Avg muscle % of live wt	Avg hepatopancreas % of live wt +SE
3	5	M	Ambient	None	<2	589	22.5	5.22±0.12
4	5	F	"	"	<2	546	24.6	5.24±0.12
11	5	M	"	H/B	140	514	24.9	4.98±0.14
15	5	M	"	None	140	590	16.2	2.64±0.41

TABLE V. Hemolymph, muscle values, and their relationship for captive lobsters exposed to different light intensities.

										Correlation coefficients	
Group No.	No. of lobsters	Sex	Temp (*C*)	Food	Duration of captivity (*days*)	Maximum illumination (*lumens/ft²*)	Avg live wt (*g*)	Avg muscle % of live wt	Avg serum protein (*mg/ml*)	Avg hemocytes/ mm³ ×10⁴	Serum protein vs. muscle contents	Hemocytes vs. muscle contents
9	20	M	Ambient	H/B	140	None	608	25.4	61.0	3.0	−0.261	−0.084
10	16	M	"	"	140	8	567	24.3	61.8	3.03	0.119	−0.061
11	25	M	"	"	140	24	634	23.6	60.7	3.08	0.497	0.027
12	28	M	"	"	140	40	545	24.2	66.7	2.81	0.415	−0.122
13	24	M	"	None	140	None	567	18.1	31.7	1.98	0.691	0.528
14	24	M	"	"	140	8	585	18.2	30.9	2.03	0.746	0.541
15	29	M	"	"	140	24	584	17.1	26.4	1.71	0.868	0.715
16	26	M	"	"	140	40	554	17.8	29.6	1.79	0.671	0.611

TABLE VI. Wild lobsters: hemolymph, muscle values, and their relationship.

										Correlation coefficients	
Group No.	No. of lobsters	Sex	Temp (*C*)	Food	Duration of captivity (*days*)	Avg live wt (*g*)	Avg muscle % of live wt +SE	Avg serum protein (*mg/ml*) +SE	Avg hemocytes/$mm^3 \times 10^4$ +SE	Serum protein vs. muscle content	Hemocytes vs. muscle content
1	31	M	Ambient	None	<2	544	22.1	35.4	2.31	0.590	0.563
2	29	F	"	"	<2	519	19.9	27.8	2.27	0.836	0.573
1 and 2	60		"	"	<2	527	21.0±0.38	31.7±1.3	2.29±0.09	0.716	0.535
3	35	M	"	"	<2	506	22.1	52.1	2.48	0.804	0.668
4	35	F	"	"	<2	522	21.8	44.1	2.32	0.530	0.360
3 and 4	70		"	"	<2	514	21.9±0.36	48.1±2.1	2.40±0.09	0.682	0.550
5	18	M	"	"	<2	555	21.1	44.0	1.87	0.829	0.328
6	17	F	"	"	<2	550	20.5	40.0	1.85	0.726	0.369
5 and 6	35		"	"	<2	552	20.8±0.47	42.0±2.6	1.86±0.1	0.785	0.343
7	25	M	"	"	<2	578	24.9	48.3	1.84	0.739	0.285
8	26	F	"	"	<2	511	21.0	33.7	1.63	0.674	0.082
7 and 8	51		"	"	<2	544	22.9±0.45	40.8±1.8	1.73±0.1	0.811	0.247

between the muscle and the serum protein values, however, are much better than those for the hemocyte:muscle relationships, since even the group (group 4) showing the poorest relationship has a correlation coefficient significant at the 1% level (Table VI).

Regression equations were calculated for the relationship between the serum protein and muscle values of all the lobsters. The captive (groups 9 through 18) and the wild (groups 1 through 8) lobsters were considered as separate groups. The equation for the entire wild group (216 animals) was $y = 12.71 + 0.178x$ and for the entire captive group (230 animals) was $y = 16.0 + 0.139x$ (y = muscle as percentage of the live weight and x = serum protein in mg/ml of serum).

The lack of correlation occurring at the very high levels of muscle suggested that there was a maximum value for muscle and serum protein beyond which the relationship was not valid. An inspection of scatter diagrams of these data indicated that the relationship declined above 55 mg protein per ml of serum. Consequently, a second set of equations was calculated for the same groups but included only those pairs of values for which the serum protein values were 55 mg/ml or less. The equation for the captive group (157 animals) was $y = 11.65 + 0.215x$ and for the wild group (184 animals) was $y = 15.65 + 0.154x$. The regression lines drawn from these equations together with the 95% confidence belts are illustrated in Fig. 4. These lines are not greatly different from those which can be drawn for the values for all of the animals in either of the captive or wild groups; however, the second set of equations reflect more accurately the most direct part of the relationship.

An examination of all of the data suggests that the mean muscle weight of lobsters rarely exceeds 24% unless the animals are provided with a good diet coupled with restricted activity. The bulk of the mean values for the wild lobsters was between 19.9 and 23% of their live body weight. The July males (group 7) were unusual in this regard in that they had the extremely high mean muscle value of 24.9% (Table VI) the highest value for all the wild lobsters in the survey.

DISCUSSION

In contrast to the findings of Pilson (1965) for the abalone (*Haliotis corrugata*) and Masat and Musacchia (1965) for the turtle (*Chrysemys picta*), this study demonstrates that the lobster hemolymph components can be altered by changes in the diet. These changes are accompanied by similar changes in the hepatopancreas and muscle.

The utilization of these body components as food reserves suggests that protein is an important endogenous substrate in the lobster (Table II). The studies of Emerson and Duerr (1967) on the prosobranch snail (*Littorina planaxis*) show that this is not always so. They found that starvation of the snail depleted the body lipids but not the proteins or polysaccharides. The similar reduction of the lipid content of the lobster hepatopancreas during starvation (Fig. 3) indicates that protein is not the sole endogenous substrate

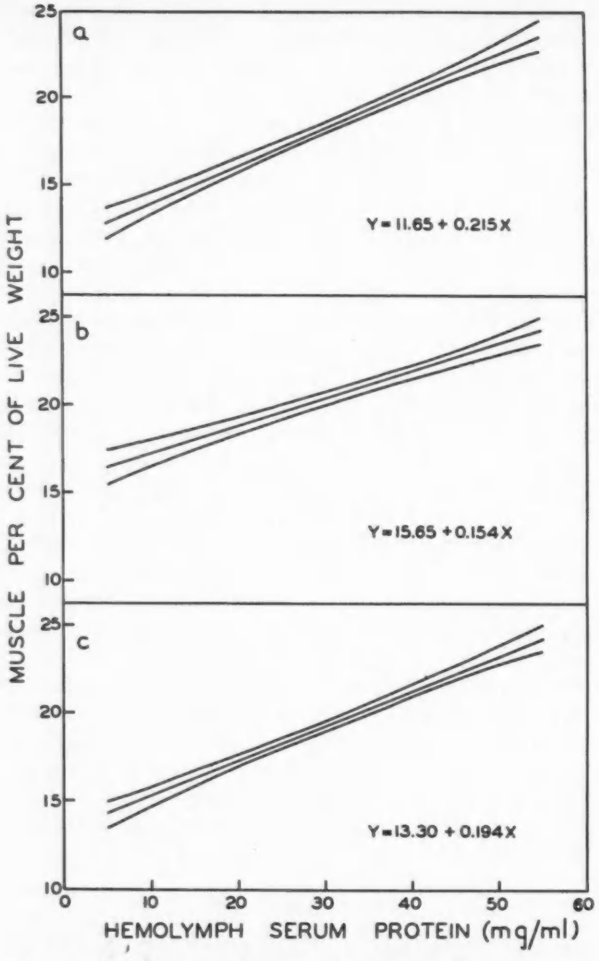


FIG. 4. Lines of regression with 95% confidence belts for serum protein (55 mg/ml or less) and muscle values for: (*a*) fed and starved captive lobsters (157 animals); (*b*) wild lobsters (184 animals); (*c*) combined captive and wild lobsters (341 animals).

for the lobster. The absence of acidic carbohydrates and glycogen in the hepatopancreatic tissue from all groups suggests that carbohydrates are not an important food reserve in this tissue. This finding is consistent with the results of Davis and Burnett (1964) for the crayfish (*Procambarus blandingii acutus*). They showed that glycogen was present in small amounts only, and then only in certain areas of the hepatopancreas.

The diffuse sudanophilic staining in the hepatopancreatic tissue taken from the captive lobsters in contrast to the more organized state of the lipid material in the wild lobsters' tissue illustrates defects in the integrity of this tissue caused by a deficient diet or starvation. This fact coupled with the lower specific gravity of the hepatopancreatic tissue from the captive fed lobsters suggests that the degeneration of this tissue results from a failure to maintain a non-lipid component. Despite this degeneration the extremely high percentage of muscle in the fed captive group indicates that no serious impairment of organ function had occurred.

The 50–70% reduction in the size of the hepatopancreas upon starvation (Table IV) is much greater than the decline in the muscle values for the same lobsters. Obviously if the site of synthesis and conversion is severely depleted the quantities of nutrients which can be processed will be limited. Thus the prolonged recovery times noted when the starved animals are permitted to resume feeding (Stewart et al., 1967) could be explained on this basis. It would be interesting to determine the relationship between hepatopancreatic recovery and the animals' return to a good physiological state.

Diet was more important than the range of temperatures or light intensities included in these experiments. Previous work has shown that beef liver plus herring fed at 14 C after starvation (Stewart et al., 1967) returned the hemocyte and plasma proteins to higher levels than did the herring diet alone. The herring diet at the lower ambient temperatures in those experiments produced very low values. In the present study the beef liver and herring diet produced considerably higher values for the hemolymph components at the lower ambient temperatures than did the herring diet at the relatively high temperature of 14 C (Table II).

Temperature, logically for a poikilothermic animal, was an important factor in starvation. All values for the lobsters starved at 14 C (Table II) were considerably lower than those for lobsters starved for twice the length of time at the lower temperatures. Although changes in plasma constituents due to temperature are not clear-cut (Stewart et al., 1966), the evidence does not indicate that the reduction in the lobsters' serum proteins was caused by hypothermia as Dean and Vernberg (1966) suggested was the case for the fiddler crab, *Uca pugilator*. The reduction in total blood proteins in the fiddler crab at a temperature which produces inactivity in this animal could be accounted for by an insignificant food intake rather than by the reduced temperature alone.

The different light intensities used in this experiment had no apparent effect on feeding behaviour as judged by the muscle, serum protein, or hemocyte values (Table V). Consequently, it would be expected that lobsters living in shoal waters would be unaffected by the more intense light as far as total food consumption is concerned. They would probably exhibit feeding rhythms different from those of lobsters living in deeper waters where the light is negligible or non-existent, but further work is required to show whether a basic feeding rhythm of the kind shown by Fielder (1965) for the spiny lobster

(*Jasus lalandei*) also exists for *H. americanus*. In addition these data do illustrate the high degree of consistency and reproducibility of the values for lobsters of the same size, sex, season, location of capture, and treatment.

The proportionate reduction of hemocyanin during starvation (Stewart et al., 1967) approaches levels which could be considered dangerously low (Table II). It is possible, however, that the efficiency of oxygen transport does not decrease linearly with decreasing hemocyanin concentration. Burton (1965) suggested that although hemolymph with higher concentrations of hemocyanin will carry more oxygen, the proportionately higher hemolymph viscosity may inpede the flow and result in only a small net oxygen gain. Thus the minimal requirement for hemocyanin could be quite low particularly for animals which, as in our experiments, were prevented or discouraged from extensive exercise by the restricted quarters. This is substantiated by the fact that the mortality rate was the same for both the starved and fed captive lobster groups. Neither did the starved animals show any obvious signs of distress, lessened activity, or even a higher incidence of cannibalism. Differences in survival time in air between fed and starved animals, however, have been shown to exist (McLeese, 1965). Experiments, such as those conducted by McLeese (1956, 1964), imposing rapid and large changes in temperature, salinity, oxygen, and exercise would be required to show whether additional differences occur.

The reports of Glavind (1948) for *Homarus vulgaris*, Lorand et al. (1963) and Stewart et al. (1966) for *H. americanus* indicate the potential danger to the animal of reduced fibrinogen and hemocyte levels. Fibrinogen and hemocyte values of wild lobsters are not always maximal (Table VI). This is of considerable importance in nature where clotting times would be prolonged not only by low concentrations of these two components but also by the low temperatures which exist for a major part of the year. These factors taken together probably account for many natural mortalities and contribute to those resulting from injuries acquired during capture.

The statistical analysis of the data showed that in all lobsters except those with very high muscle values (groups 9 through 12) the correlation between serum protein and muscle values was significant. The relationship between the hemocytes and the muscle was not as reliable as the serum protein:muscle relationship. The hemocyte levels, however, do respond more rapidly to changes in diet than do the serum protein levels (Stewart et al., 1967).

The data in Table VI demonstrate that whereas the relationship between the serum proteins and the muscle is always significant it is not always the same; consequently, regression lines drawn for the different groups would have different slopes and intercepts. The conclusion based on the limited data is that differences resulting from area of capture are more important than the seasonal differences.

The differences in the serum protein:muscle relationships attributable to sex are less consistent (Table VI). The correlation coefficient for males (group 1) is less significant than that for females (group 2) captured at the same time from the same area. The reverse situation occurs for groups 3 and 4 where the females show the poorer relationship.

The regression relationships illustrated in Fig. 4 show that when animals of identical sex, area, and date of capture are used in a nutritional experiment the relationship is excellent. This relationship has been improved by using only those serum protein values equal to or less than 55 mg/ml of hemolymph; the maximum protein value corresponds to a muscle value of approximately 24% of the live animals' weight. The regression line representing the data for the wild lobsters shows that regardless of area of capture, sex, or season the overall relationship is sound. Thus the use of serum protein values as an index of the effectiveness of the diet is validated, The authors' intention is to apply this technique in determining the nutritional requirements of the lobster and to use it, keeping in an mind its limitations, in assessment of the physiological changes in wild lobsters.

ACKNOWLEDGMENTS

We thank Dr H. Brockerhoff and Dr A. S. Grimm for their constructive criticism of the manuscript and Mr Lloyd MacDonald, Fourchu, N.S., of the Department of Fisheries of Canada, for his assistance in obtaining large numbers of lobsters. We gratefully acknowledge the assistance of Mr R. A. Hornstein, Officer in Charge, Atlantic Weather Central, Halifax, N.S., who supplied data on the number of hours of daylight and sunshine occurring throughout the year in this area.

REFERENCES

Burton, R. F. 1965. Possible factors limiting the concentration of hemocyanin in the blood of the snail, *Helix pomatia* L. Canadian J. Zool., **43**: 433–438.

Davis, L. E., and A. L. Burnett. 1964. A study of growth and cell differentiation in the hepatopancreas of the crayfish. Develop. Biol., **10**: 122–153.

Dean, J. M., and J. F. Vernberg. 1966. Hypothermia and blood of crabs. Comp. Biochem. Physiol., **17**: 19–22.

Dixon, W. J., and F. J. Massey, Jr. 1951. Introduction to statistical analysis. McGraw-Hill Book Company, Inc., New York.

Emerson, D. N., and F. G. Duerr. 1967. Some physiological effects of starvation in the intertidal prosobranch *Littorina planaxis* (Philippi, 1847). Comp. Biochem. Physiol., **20**: 45–53.

Fielder, D. R. 1965. The spiny lobster, *Jasus lalandei* (H. Milne-Edwards), in South Australia III. Food, feeding and locomotor activity. Australasian J. Marine Freshwater Res., **16**: 351–367.

Glavind, J. 1948. Studies on the coagulation of crustacean blood. Nyt Nordisk Forlag, Arnold Busck, Copenhagen.

Goulden, C. H. 1952. Methods of statistical analysis. John Wiley and Sons Inc., New York.

Herrick, F. H. 1911. Natural history of the American lobster. Bull. U.S. Bur. Fish., **29**: 149–408.

HUMASON, G. L. 1962. Animal tissue techniques. W. H. Freeman and Company, San Francisco, Calif.

KIMBALL, H. H. 1928. Amount of solar radiation that reaches the surface of the earth on the land and on the sea, and the methods by which it is measured. Monthly Weather Rev., **56**: 393–398.

KLUGH, A. B. 1927. Light penetration into the Bay of Fundy and into Chamcook Lake, New Brunswick. Ecology, **8**: 90–93.

LAUFFER, M. A., AND L. G. SWABY. 1955. The size, shape, and hydration of lobster hemocyanin. Biol. Bull., **108**: 290–295.

LAYNE, E. 1957. Spectrophotometric and turbidimetric methods for measuring proteins. *In* S. P. Colowick, and N. O. Kaplan, [ed.] Methods in enzymology, Vol. 3. Academic Press, Inc., New York. p. 450.

LORAND, L., R. F. DOOLITTLE, K. KONISHI, AND S. K. RIGGS. 1963. A new class of blood coagulation inhibitors. Arch. Biochem. Biophys., **102**: 171–179.

MASAT, R. J., AND X. J. MUSACCHIA. 1965. Serum protein concentration changes in the turtle, *Chrysemys picta*. Comp. Biochem. Physiol., **16**: 215–225.

MCLEESE, D. W. 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. J. Fish. Res. Bd. Canada, **13**: 247–272.
1964. Oxygen consumption of the lobster, *Homarus americanus* Milne-Edwards. Helgolaender Wiss. Meeresuntersuch., **10**: 7–18.
1965. Survival of lobsters, *Homarus americanus*, out of water. J. Fish. Res. Bd. Canada, **22**: 385–394.

PILSON, M. E. Q. 1965. Variation of hemocyanin concentration in the blood of four species of *Haliotis*. Biol. Bull., **128**: 459–472.

STEWART, J. E. 1963. An arrangement for automatically and reproducibly controlling and varying illumination in biological experiments. J. Fish. Res. Bd. Canada, **20**: 1103–1107.

STEWART, J. E., J. W. CORNICK, AND J. R. DINGLE. 1967. An electronic method for counting lobster (*Homarus americanus* Milne-Edwards) hemocytes and the influence of diet on hemocyte numbers and hemolymph proteins. Canadian J. Zool., **45**: 291–304.

STEWART, J. E., P. H. ODENSE, AND J. R. DINGLE. 1966. Constituents of the hemolymph of the lobster, *Homarus americanus* Milne-Edwards. Canadian J. Biochem., **44**: 1447–1459.

STEWART, J. E., AND H. E. POWER. 1963. A sea water aquarium for marine animal experiments. J. Fish. Res. Bd. Canada, **20**: 1081–1084.

THOMAS, H. J. 1958. Lobster storage. Scottish Home Dept., H. M. Stationery Office. 20 p.

WILDER, D. G., AND D. W. MCLEESE. 1961. A comparison of three methods of inactivating lobster claws. J. Fish. Res. Bd. Canada, **18**: 367–375.

A Mathematical Model of Some Aspects of Fish Growth, Respiration, and Mortality[1]

By Erik Ursin

Danish Institute for Fishery and Marine Research
Charlottenlund, Denmark

ABSTRACT

A simple metabolic model describing growth as the difference between what enters the body and what leaves it, is elaborated assuming that synthetic processes (the building-up, the anabolism) are consuming energy supplied by processes of decomposition (the break-down, the catabolism). This leads to partitioning total catabolism into two components, one being a function of the rate of synthesis, another keeping the body functioning independently of synthesis. The rate of synthesis is described as a function of food taken, of the efficiencies of digestion and energy conversion, and of the absorbing surface of the intestine. Catabolic processes are supposed to be functions of the oxygen concentration in the water, the absorbing surface of the gills, and the rate of oxygen transport. Both kinds of processes are made functions of temperature in the way enzymatic processes usually are. Assuming that molecular interactions accidentally go wrong makes natural mortality, like growth, a function of the rates of anabolic and catabolic processes and body size.

Application of the model to data of length-at-age, food and oxygen consumption, weight loss, gill area, and natural mortality indicates that at least some of the main hypotheses cannot be rejected on available evidence.

INTRODUCTION

THE METABOLIC growth model was advanced by Pütter (1920), the first to realize the usefulnes of the truism, that what remains in the body is the difference between what comes in and what goes out. The rate of intake of food, he considered, must be surface dependent whereas the rate of break-down, occurring everywhere in the body, must depend on body weight. Thus:

$$dw/dt = \mathrm{H}\, w^{2/3} - k\, w \qquad \ldots\ldots(1)$$

If w is the weight in grams and t the time in seconds, the coefficient of anabolism, H, has the dimension $g^{1/3}$ sec,$^{-1}$ and the coefficient of catabolism is k sec^{-1}. Pütter's paper is a remarkably early attempt at turning natural history into science through a mathematical modelling of biological phenomena.

The work was continued by von Bertalanffy in his original papers (1934, 1938) and in several more recent ones (e.g., 1964). Other developments were made by Beverton and Holt (1957, 1959), Taylor (1958, 1962), and most recently by Paloheimo and Dickie (1965, 1966a, b). Independently, a similar model was developed for unicellular organisms by Rashevsky (1960), operating on the molecular level. The metabolic model has been abundantly

---

[1] Received for publication February 6, 1967.

J. Fish. Res. Bd. Canada, 24(11), 1967.
Printed in Canada.

applied, particularly in fishery biology, but a gap has developed between the students of growth and the physiologists developing empirical models of metabolic phenomena (e.g. Winberg, 1956, 1962; Ivlev, 1961a, b), this, apparently, because the relationship between growth and respiration has remained insufficiently known. The present paper is a faltering attempt towards a better understanding of these interrelations.

The notation is rather extensive. To aid memory, the symbols used are listed and explained in Appendix I.

In the first part of the paper a model is developed on the assumption that the fish lives in an entirely stable environment. In the sections following, the model is elaborated to allow for differences in food supply, temperature, and oxygen contents of the water. An additional hypothesis on metabolic processes as a cause of natural mortality is also developed. Finally, the links to a less elaborate, but in fact very similar model by Winberg are indicated.

Admittedly, the model is hard to perceive because of the large number of parameters successively introduced. On the other hand, I *think* it has one virtue: that of being consistent with itself.

Quite another problem is whether the model has anything to do with the real world. That is investigated in Appendixes II–XIV, where various sorts of data, mostly from literature, are fitted to appropriate parts of the model in order to find out if the various hypotheses advanced can be rejected. It is not attempted to prove the hypotheses. With the approach to scientific method adopted here nothing can be proved, but a hypothesis can be rejected when it is shown with a high degree of probability to be false. When a rejected hypothesis is part of a more extensive model, one must accept the observed limitations of the applicability, or the involved part of the model must be broken down and advanced in another shape. The model below was developed that way. With this approach the same set of data can fail to reject any of two alternative hypotheses, and particularly, when the information is veiled by large measuring errors. The idea is that until we obtain possession of material which can reject the hypothesis, the latter is good enough for our purpose.

It was intended to develop the model by reasoning only, but it soon became apparent that émpirical relationships had to be incorporated here and there. Mathematical approximations were used frequently, too, in order to simplify expressions which are difficult to handle. The two methods, the use of empirical relationships and of mathematical approximations, are closely related. In both cases, the first approximation is a single point (say, a mean value) and the second a straight line (a tangent or secant of any curve). Only the third and consecutive approximations provide the choice of various possibilities of which the exponential function (i.e., a per cent change) often seems the simplest.

A third kind of approximations comes in useful after a model has been developed. Scrutiny of the model reveals situations when replacement of certain variables by constants provides simple relationships (linear, parabolic, ect.) between two quantities. A good experimental set-up in which the variables in question are kept reasonably constant and where the two quantities can be measured leads to rejection of the hypothesis in a large part of the cases when it is false.

Another important method of testing hypotheses is to estimate the same parameter in different ways and compare the results. This approach has been used extensively in the present paper.

A really up-to-date account should deal with the energy transfer on a molecular level, a subject, however, which I do not master. Instead, I shall deal with changes of mass, and under the following assumptions:

that the specific gravity of the fish is equal to one ($g = cm^3$);

that the proportions of the body are constant (isometric growth: surface $= q' l^2$, weight $= q l^3$, where l is length (exceptions are made for absorbing surfaces);

that the food has the same chemical constitution as the fish;

that the synthetic processes have negative entropy (are not spontaneous); and

that the energy necessary for these processes is supplied by oxidations requiring free oxygen.

These assumptions were made in order to simplify the model.

THE METABOLIC GROWTH MODEL

A. THE BASIC EQUATION

Generalized, Pütter's model (equation 1) becomes

$$dw/dt = \Phi\,(dR/dt) - \Gamma\,(w, \Phi\,(dR/dt)) \qquad \ldots\ldots(A1)$$

where w is weight, dR/dt the food consumed in unit time, and t time. The equation expresses that the quantity absorbed is a function of the quantity eaten, whereas the quantity lost is a function of (1) the size of the fish, because even in a fasting fish every cell must metabolize to remain alive; and (2) of the food absorbed, because digesting and assimilating food require energy.

By writing the left-hand side of equation A1 as an ordinary differential equation instead of a partial one, it is specified that we are assuming that the growth rate is a function of body weight and time and of these only. That means that if ration is a function of anything but weight and time (e.g. of the food concentration in the water) fixed values of other variables must be chosen before integrating. As shown below, ration can, and, indeed, in a marginal situation must be written as a function of body size because there is an upper limit to what a fish of a given size can eat.

In this paper the right-hand terms of equation A1 shall be called "the anabolic term" (the first one) and "the catabolic term" (the second one).

Let it be assumed for the moment that the food consumed is completely digested and that the intestine is always full. This is the marginal situation mentioned above. The quantity absorbed now is proportional with the absorbing surface which, in case of isometric growth, is proportional with $w^{2/3}$. The area of the intestine and, indeed, its inner surface, is tricky to measure because postmortal changes occur. A few pilot experiments were rather discouraging, e.g., from measurement of eight soles (*Solea solea*) the outer surface of the intestine was estimated as

$$2.12\ w^{0.57}\ \mathrm{cm}^2$$

where the superscript, 0.57, has a 95% confidence interval from 0.33 to 0.80. Until more becomes known of this subject we shall cautiously put, in equation A1,

$$\Phi\ (d\mathrm{R}/dt) = d\mathrm{R}/dt = dr/dt = h_1\ w^m \qquad \ldots\ldots(\mathrm{A2})$$

where dr is the quantity absorbed from the intestine. Equation A2 describes total, or gross, anabolism as it is supposed to be when the intestine is full and the food is completely digested. What may happen when the fish is given restricted rations and when digestion is not complete is discussed in a later paragraph (Growth and Food).

The catabolic term of equation A1, $-\Gamma(w,\ \Phi\ (d\mathrm{R}/dt))$, can be assumed to consist of two additive terms representing (1) the catabolism of a fasting fish (we shall call it "the fasting catabolism"); and (2) the extra catabolism necessitated by feeding ("the feeding catabolism"), partly because mechanical work is involved in eating and digestion, and partly because an extra breakdown is necessary to supply free energy for synthesis of tissue. Fasting catabolism plus feeding catabolism make up the total catabolism of a fed fish. We shall assume that fasting catabolism depends on the size of the fish only and that feeding catabolism depends on the quantity of food absorbed only and constitutes a constant fraction, α, of gross anabolism. Of course, more elaborate models can be made, but it is not attempted here. The size of α is determined by the heat loss (the inefficiency of energy transfer) and the loss of energy through the urine. Casey (1962, p. 173 and 178) considers an energy transfer loss of 63% (observed in the human respiratory enzyme system) as a probable upper limit (i.e., $\alpha \geq 0.63$) whereas Winberg (1956) finds that yolk energy is transferred to the fish foetus with a loss of only 35% ($\alpha = 0.35$). The energy loss through urine seems to be insufficiently known at present. Thus, the lowest value of α to be expected is 0.35 whereas values twice as high are more likely to be met with. α is estimated in Appendix VII.

According to the foregoing we can write

$$-\ \Gamma\ (w,\ \Phi\ (d\mathrm{R}/dt)) = -\ \varphi\ (w) - \gamma\ (dr/dt) \qquad \ldots\ldots(\mathrm{A3})$$

where the first of the right-hand terms represents the fasting catabolism and the second term represents the feeding catabolism. By means of equation A2, the latter can be expanded as

$$-\ \gamma\ (dr/dt) = -\ \alpha\ h_1\ w^m \qquad \ldots\ldots(\mathrm{A4}).$$

Note that here, as elsewhere in the paper, expressions for catabolism are given a negative sign. In other words: growth is considered the sum of the effects of anabolism and catabolism, the latter being negative. Thus, the net anabolism can be defined as the sum of gross anabolism (equation A2) and feeding catabolism (equation A4):

$$\Phi\,(dR/dt) - \gamma\,(dr/dt) = h_1\,w^m - \alpha\,h_1\,w^m = (1-\alpha)\,h_1\,w^m = \mathrm{H}\,w^m \quad \ldots(\mathrm{A5})$$

still on the assumption that the intestine is always full and the food completely digested. Putting $m = 2/3$ gives the anabolic term, $\mathrm{H}\,w^{2/3}$ of Pütter's approximation, equation 1.

The fasting catabolism, $-\varphi(w)$, equals Pütter's catabolic term, $-kw$, and is the rate of weight loss of a fish behaving normally. Putting $\varphi(w) = k\,w$ as Pütter did, is unsatisfactory because there is now sufficient evidence from respiration experiments that fasting catabolism is not usually proportional with weight. Apparently, it was overlooked that although catabolic processes are going on all over the body, the necessary oxygen supply has to be introduced through some surface or other, mainly the gills. With our basic assumption of isometric growth this means that catabolism is proportional with $w^{2/3}$. As discussed in several of the Appendixes, this is also known to be untrue, so that the assumption of isometric growth must be abandoned for the occasion. In fact (App. XIV) the gills do not grow isometrically with the body, because new units are being added as the fish grows. Retaining the assumption of isometric growth of the body as a whole we can describe the surface areas of body and gills by

$$\left.\begin{aligned} \mathrm{S}_b &= \mathrm{A}_b\,w^{2/3} \\ \mathrm{S}_g &= \mathrm{A}_g\,w^{n_g} \end{aligned}\right\} \quad \ldots\ldots(\mathrm{A6}).$$

The rates of respiration of a fasting fish through skin and gills are

$$\left.\begin{aligned} (d\mathrm{O}_2/dt)_b &= -\,\mathrm{B}_b\,\mathrm{S}_b \\ (d\mathrm{O}_2/dt)_g &= -\,\mathrm{B}_g\,\mathrm{S}_g \end{aligned}\right\} \quad \ldots\ldots(\mathrm{A7})$$

where $-\mathrm{B}_b$ and $-\mathrm{B}_g$ are the rates of oxygen consumption in unit time and area. Total fasting respiration becomes

$$(d\mathrm{O}_2/dt)_{fasting} = -\,(\mathrm{B}_b\,\mathrm{A}_b\,w^{2/3} + \mathrm{B}_g\,\mathrm{A}_g\,w^{n_g} \approx -\,\omega\,k\,w^n \quad \ldots\ldots(\mathrm{A8})$$

where $2/3 < n < n_g$. The reason for factoring the right hand constant into ω and k emerges when ω is defined as the proportionality constant relating the oxygen consumption of a fasting animal to weight loss,

$$\omega = d\mathrm{O}_2/dw.$$

Returning to equation A3 we can now put

$$-\varphi(w) = \frac{1}{\omega}(dO_2/dt)_{fasting} = (dw/dt)_{fasting} = -k\,w^n \quad \ldots\ldots(A9).$$

ω and n are dimensionless. k is a proper rate constant (dimension, time^{-1}) only for $n = 1$. Otherwise it has the obscure dimension of $\text{weight}^{1-n}\ \text{time}^{-1}$.

The rate of feeding catabolism, expressed as weight loss, was found to be

$$-\gamma\,(dR/dt) = -\alpha\,h_1\,w^m \quad \ldots\ldots(A4).$$

The corresponding oxygen consumption is

$$(dO_2/dt)_{feeding} = \omega\,(dw/dt)_{feeding} = -\omega\,\alpha\,h_1\,w^m \quad \ldots\ldots(A10).$$

Adding equation A9 to equation A10 gives the oxygen consumption of fed fish as

$$(dO_2/dt)_{fed} = (dO_2/dt)_{feeding} + (dO_2/dt)_{fasting} = -\omega\,\alpha\,h_1\,w^m - \omega\,k\,w^n \quad \ldots\ldots(A11).$$

$\omega\alpha h_1$, ωk, m, and n are estimated from oxygen consumption data in App. IV; ω is estimated in App. V.

There is one difficulty with equation A8 which has been passed over tacitly above, as elsewhere in the paper. It was assumed, in fact, that any change in the oxygen consumption due to activity or temperature changes causes proportional change in gill respiration and skin respiration. This, however, is not to be expected. Increased respiration probably to a large extent is effected by an increased rate of ventilation of the gills. Thus B_g will increase more than B_b and not only k (on the right-hand side) will increase, but so will n. The same reasoning applies to the oxygen consumption of a fed fish: a higher proportion of the oxygen passes through the gills than in a fasting one. This does not cause much trouble, though, because the total oxygen consumption of a fed fish is regulated by the rate of food consumption which is proportional with a low power, m, of w. Other complications, masking the effect of increased gill respiration probably occur. For instance, it is doubtful whether the rate of gill ventilation can in practice be altered proportionally with the oxygen demand in fish of all sizes when temperature or activity increases. If it cannot, n_g is not constant. To elucidate these things would mean to build a detailed model of gill respiration which is not attempted here.

Equation A11 is often sucessfully approximated by a single exponential term,

$$dO_2/dt = -D\,w^d \quad \ldots\ldots(A12)$$

which is valid whether the fish has eaten or not (see App. II and IV). d attains values between m and n. The energy equivalent of equation A12 is the metabolic term, T, of Winberg's (1956, p. 209) growth equation.

Evaluating k from weight loss data for fasting fishes is simplest by integrating equation A9:

$$(dw/dt)_{fasting} = -\,k\,w_n \qquad \ldots\ldots(\mathrm{A9})$$

$$w_t^{\,1-n} = w_o^{\,1-n} - (1-n)\;{}_nk\;t\;(n\neq 1) \qquad \ldots\ldots(\mathrm{A13})$$

$$ln\;w_t = ln\;w_o - {}_1k\;t\;(n=1) \qquad \ldots\ldots(\mathrm{A14})$$

where w_o is the initial weight. The subscripts, n and 1, of k were introduced to distinguish between estimates based on A13 and A14. Given two points, $(w_o,\,0)$ and $(w_t,\,t)$, through which all curves determined by equations A13 and A14 must go, the computation of ${}_nk$ (i.e., of k for $n\neq 1$) is often facilitated by eliminating t from equations A13 and A14, putting $w_t = \mathrm{C}\,w_o$ (C slightly smaller than one) and putting

$$\frac{\mathrm{C}^{1-n}-1}{(1-n)\;ln\;\mathrm{C}} = 1.$$

This leads to

$$ln\;{}_nk = ln\;{}_1k + (1-n)\;ln\;w_o \qquad \ldots\ldots(\mathrm{A15})$$

which with equation A14 gives quick solutions for ${}_nk$. They are often very accurate because the curves described by equations A13 and A14 are almost straight lines for weight losses of, say, up to 20%.

In practice, n cannot be estimated from individual fasting experiments. This is another effect of equations A13 and A14 being practically linear. Data for a wide range of weight (several fasting experiments with fish of different size) are necessary for estimating n (see Appendix IX). Parameter estimates from the weight loss of fasting fishes are made in App. VIII and IX.

According to the foregoing we have

$$\begin{aligned} dw/dt &= \Phi\,(d\mathrm{R}/dt) - \Gamma\,(w,\,\Phi\,(d\mathrm{R}/dt)) \\ &= \Phi\,(d\mathrm{R}/dt) - \gamma\,(dr/dt) - \varphi\,(w) \\ &= h_1\,w_m - \alpha\,h_1\,w^m - k\,w^n \\ &= (1-\alpha)\,h_1\,w^m - k\,w^n \\ &= \mathrm{H}w^m - k\,w^n \qquad \ldots\ldots(\mathrm{A16}). \end{aligned}$$

Reducing to the linear dimension gives

$$\frac{dw^{1/3}}{dt} = \frac{\mathrm{H}}{3}\,w^{m-2/3} - \frac{k}{3}\,w^{n-2/3} \qquad \ldots\ldots(\mathrm{A17})$$

because

$$\frac{dw^{1/3}}{dt} = \frac{1}{3}w^{-2/3}\,\frac{dw}{dt}.$$

Putting, in accordance with an assumption made in the introduction, $w = ql^3$, where l is body length, equation A16 becomes

$$\frac{dl}{dt} = \frac{\mathrm{H}}{3q^{1-m}}\, l^{3m-2} - \frac{k}{3q^{1-n}}\, l^{3n-2} = \mathrm{E}l^{3m-2} - \mathrm{K}l^{3n-2} \qquad \text{.....(A18)}$$

where E and K are constants.

When the increment, dw/dt or dl/dt, is zero, the fish has reached its asymptotic size. Equations A16 and A18 give

$$\mathrm{W}_\infty = \left(\frac{\mathrm{H}}{k}\right)^{\frac{1}{n-m}} \qquad \text{.....(A19)}$$

$$\mathrm{L}_\infty = q^{-1/3}\left(\frac{\mathrm{H}}{k}\right)^{\frac{1}{3(n-m)}} = \left(\frac{\mathrm{E}}{\mathrm{K}}\right)^{\frac{1}{3(n-m)}} \qquad \text{.....(A20)}$$

where W_∞ is the asymptotic weight and L_∞ the asymptotic length.

Paloheimo and Dickie (1965) found empirically that fish growth is not asymptotic which raises the question whether W_∞ and L_∞ are artefacts, brought into existence by introducing approximations. This is quite possible because the exponential expressions (equations A2 and A9) for anabolism and catabolism are approximative only.

Inflections on the growth curves are found by differentiating equations A16 and A18 and putting the derivatives equal to zero, e.g.,

$$\frac{dl}{dt} = \mathrm{E}l^{3m-2} - \mathrm{K}l^{3n-2} \qquad \text{.....(A18)}$$

$$\frac{d^2l}{dt^2} = \left((3m-2)\ \mathrm{E}l^{3(m-1)} - (3n-2)\ \mathrm{K}l^{3(n-1)}\right)\frac{dl}{dt} \qquad \text{.....(A19)}$$

$$(3m-2)\ \mathrm{EL_I}^{3(m-1)} - (3n-2)\ \mathrm{KL_I}^{3(n-1)} = 0 \qquad \text{.....(A20)}$$

$$\mathrm{L_I} = \left(\frac{3m-2}{3n-2}\,\frac{\mathrm{E}}{\mathrm{K}}\right)^{\frac{1}{3(n-m)}} = \mathrm{L}_\infty\left(\frac{3m-2}{3n-2}\right)^{\frac{1}{3(n-m)}} \qquad \text{.....(A21)}$$

and similarly

$$\mathrm{W_I} = \mathrm{W}_\infty\left(\frac{m}{n}\right)^{\frac{1}{(n-m)}} \qquad \text{.....(A22).}$$

The weight curve is inflected for all values of m and n while the length curve has an inflection for $m > 2/3$ only. Estimates of m, based on the assumption

$w = ql^3$ so far have given values about or below 2/3 so that appreciable inflection of the length curve can scarcely be expected. Taylor (1962), however, has shown that the generalization $w = ql^C$ leads to inflected length curves for $C \neq 3$ (anisometric growth).

The approximation, $m = 2/3$, $n = 1$, leads to Pütter's growth equation (equation 1) which has several virtues. It lends the simple physical dimensions of speed and rate (length time^{-1} and time^{-1}) to H and k. It is easily integrated (elegantly by Beverton and Holt, 1957) while for most other values of m and n integration must be made numerically. Astoundingly, it also very often provides a fine representation of growth data which has ensured it a wide application in the yield assessments of fishery biologists. Its main limitation is that further reasoning on physiological lines often leads the investigator astray so that his hypotheses are easily rejected by experiment. The assumption of weight proportionality of catabolism, for instance, is seldom acceptable in respiration studies.

With Pütter's approximation we have

$$\frac{dw}{dt} = Hw^{2/3} - kw \qquad .....(1)$$

$$\frac{dl}{dt} = E - Kl \qquad .....(A23)$$

$$W_\infty = \left(\frac{H}{k}\right)^3 \qquad .....(A24)$$

$$L_\infty = \frac{E}{K} \qquad .....(A25)$$

$$W_I = \frac{8}{27} W_\infty \qquad .....(A26)$$

$$l_t = L_\infty \, (1-e^{-K(t-t_o)}) \qquad .....(A27)$$

$$w_t = W_\infty \, (1-e^{-K(t-t_o)})^3 \qquad .....(A28)$$

where $K = \frac{k}{3}$, and t_o is the time when $l_t = 0$. The estimation of t_o is not dealt with in the present paper. The reader is referred to Beverton and Holt (1957, p. 284.)

B. GROWTH AND FOOD

In the first paragraph it was assumed that the fish had always eaten as much as it possibly could and that all what it ate was absorbed by the intestine.

We shall now look into the situation when the fish has opportunity to eat only a fraction of the highest possible ration and when a fraction of the food is discarded as excrements. To that end two new parameters shall be defined, namely, f, the feeding level, and β, the fraction absorbed of the food eaten.

The feeding level, f, we shall define as the fraction eaten of the quantity which could possibly be eaten. The latter is given by equation A2:

$$dR/dt = h_1 w^m$$

so that

$$f = \frac{dR/dt}{h_1\ w^m} \qquad \ldots\ldots(B1)$$

and equation A2 can be re-written as

$$dR/dt = h_1 f\, w^m \qquad \ldots\ldots(B2).$$

The fraction, β, absorbed of the food eaten can be considered constant as Winberg (1956) does, putting $\beta = 0.8$ in which, however, is included the energy losses with the urine. In the present model these are incorporated in α. Most authors, however, consider β a decreasing function of the feeding level. Brody and Procter (1933) (cited in Brody, 1945, p. 78) and Kostitzin (1937, p. 163) developed empirical models which, however different they may look, are very like each other.

Kostitzin's model was applied by Beverton and Holt (1957, p. 113). In both, the maximum utilization of food is low because the weight loss during energy transfer and other losses are implicit, whereas in the model developed in the preceding paragraph they are given explicitly as the collective term, $-\gamma\ (dr/dt)$, of equation A3. Thus, neither Brody's nor Kostitzin's formulations are directly applicable and must be replaced by a more appropriate formulation. The development of a realistic model of the mechanics and chemistry of digestion is probably premature so that any attack on the problem has to be largely empirical. I have made some simple reasoning which is not, however, proof against a rigorous mathematical criticism. It led to a simple function

$$\beta = 1\text{–}e^{-h_2/f} \qquad \ldots\ldots(B3)$$

which has largely the properties one would require of β. At maximum feeding ($f = 1$) the fraction absorbed is minimum: $\beta = 1\text{–}e^{-h_2}$. For $f \rightarrow 0$, $\beta \rightarrow 1$. Equation B3 is applied to data in App. VII and seems to work satisfactorily. The new parameter, h_2. has no dimension.

In a more general form equation A2 now can be written

$$\Phi\ (dR/dt) = dr/dt = \beta\, dR/dt = h_1 f\, \beta\, w^m = h\, w^m \qquad \ldots\ldots(B4).$$

The present and preceeding paragraphs can be summarized as follows:

$$\textit{Feeding level} = f = \frac{dR/dt}{h_1\ w^m} \qquad \text{.....(B1)}$$

$$\textit{Rate of feeding} = \textit{ration eaten} = dR/dt = h_1\, fw^m \qquad \text{.....(B2)}$$

$$\textit{Fraction absorbed of food eaten} = \beta = 1\text{-}e^{-h_2/f} \qquad \text{.....(B3)}$$

Rate of gross anabolism = *ration absorbed* =

$$\Phi\ (dR/dt) = dr/dt = \beta\ dR/dt = h_1\, f\, \beta\, w^m = hw^m \qquad \text{.....(B4)}$$

$$\textit{Rate of net anabolism} = \textit{gain} = (1-\alpha)\ dr/dt \qquad \text{.....(B5)}$$

$$\textit{Rate of feeding catabolism} = -\alpha\ dr/dt \qquad \text{.....(B6)}$$

$$\textit{Rate of fasting catabolism} = -\ kw^n \qquad \text{.....(B7)}$$

Rate of growth =

$$dw/dt = (1-\alpha)\frac{dr}{dt} - kw^n = (1-\alpha)\ h_1\, f\, \beta\, w^m - kw^n = \mathrm{H}w^m - kw^n \qquad \text{.....(B8)}$$

Equation B8 contains a detailed expression for the

Instantaneous coefficient of net anabolism =

$$\mathrm{H} = (1-\alpha)\ (1\text{-}e^{-h_2/f})h_1\, f = (1-\alpha)\ \beta\, h_1\, f = v\, h_1\, f \qquad \text{.....(B9)}$$

In the interpretation of v, see equation B20. In the simple model developed in the preceding paragraph we had $\mathrm{H} = (1-\alpha)h_1$ (equation A16) because $f = 1$ and $\beta = 1$ by definition. Equations A17–A28 remain valid in the more elaborate model of the present paragraph when the expanded expression for H, equation B9, is inserted.

An interesting point is the determination of the maintenance ration, i.e. the ration allowing the fish just to maintain its weight. The problem has two aspects. One is to find the ration to be given in order to keep the body weight constant, another to find how much of a bigger ration will be used for maintenance purposes. In the former case the feeding level, f, is a function of body size because a fish which has grown as big as it can will need full ration ($f = 1$) to keep its weight up. A smaller fish must be given a comparatively smaller ration ($f < 1$; $f \rightarrow 0$ for $w \rightarrow 0$) to prevent it from growing further. In fact, giving maintenance ration to a fish which has not reached its potential full size amounts to putting its present weight equal to W_∞.

In the case where a fish is fed more than maintenance ration, the feeding level is independent of body size (f = constant) and, accordingly β, the fraction absorbed of the food eaten, is constant. In the other case β varies with body size because it is a function of f.

Basically, the maintenance ration must make up for the weight loss, $-k\ w^n$ (e.g. gram per day), but in order to synthesize a similar amount, kw, of tissue some energy is wasted in the activities of acquiring and synthesizing it. Thus, the rate of dissipation of matter in the body is the sum of the fasting catabolism and the fraction α of the maintenance food absorbed. The maintenance ration to be absorbed therefore is

$$\left(\frac{dr}{dt}\right)_{maint} = \alpha\left(\frac{dr}{dt}\right)_{maint} + kw^n \qquad \ldots\ldots(\mathrm{B10})$$

from which

$$(dr/dt)_{maint} = kw^n/(1-\alpha) \qquad \ldots\ldots(\mathrm{B11}).$$

From this point of the analysis the attention must be divided between the two situations discussed above. First, assume that the fish is fed maintenance ration and not more than that. We can put $w = \mathrm{W}_\infty$ and $\beta = \mathrm{g}\ (f)$ must be specified as $\beta_{maint} = \mathrm{g}'(\mathrm{W}_\infty)$ because now $f = f_{maint} = \mathrm{g}''\ (\mathrm{W}_\infty)$. By means of equations B4 and B11 we have

$$\beta_{maint}\left(\frac{d\mathrm{R}}{dt}\right)_{maint} = \left(\frac{dr}{dt}\right)_{maint} = \frac{k\ \mathrm{W}_\infty^n}{1-\alpha} \quad \text{and the}$$

$$\textit{Maintenance ration} = (d\mathrm{R}/dt)_{maint} = \frac{k\mathrm{W}_\infty^n}{(1-\alpha)\beta_{maint}} \qquad \ldots\ldots(\mathrm{B12}).$$

β_{maint} decreases when W_∞ increases. Using a crude approximation we can put

$$\beta_{maint} = \mathrm{C}_1\ \mathrm{W}_\infty^{-\mathrm{C}_2}\ (\mathrm{C}_1 \text{ and } \mathrm{C}_2 \text{ positive})$$

from which

$$(d\mathrm{R}/dt)_{maint} = \frac{k}{\mathrm{C}_1\,(1-\alpha)}\ \mathrm{W}_\infty^{\ n+\mathrm{C}_2} \qquad \ldots\ldots(\mathrm{B13})$$

indicating, that a plot of log maintenance ration against log body weight has a slope $>n$ if C_2 is significant. A slope $<n$ should not be possible. For an application of equation B13, see App. VII.

Maintenance ration can also be defined by means of equation B2, writing

$$(d\mathrm{R}/dt)_{maint} = h_1\, f_{maint}\ \mathrm{W}_\infty^m \qquad \ldots\ldots(\mathrm{B14})$$

which is permissible because the maintenance ration is the whole ration taken. f_{maint} is a function of w and is found by putting dw/dt equal to zero in equation B8 and solving for f. Thus,

$$\textit{Maintenance feeding level} = f_{maint} = \frac{k\ w^n}{(1-\alpha)\ \beta\ h_1\ w^m} = \frac{k}{v\ h_1}\ w^{n-m} \quad \ldots\ldots(\mathrm{B15}).$$

In the other situation to be considered, in which the actual ration given is above maintenance ration, equation B11 can be written

$$\beta\left(\frac{dR}{dt}\right)_{mr} = \left(\frac{dr}{dt}\right)_{mr} = \frac{kw^n}{1-\alpha} = \left(\frac{dr}{dt}\right)_{maint}$$

and we have the

$$\textit{Maintenance requirements} = (dR/dt)_{mr} = \frac{kw^n}{(1-\alpha)\beta} = kw^n/v \quad \ldots\ldots(B16)$$

where β is independent of body size but remains a function of the feeding level, f. v is defined below (equation B20). The higher f is, the smaller is β and the higher the maintenance requirements for fish of any size. Corresponding to each feeding level there is one value of w (the highest) for which $w = W_\infty$, $\beta = \beta_{maint}$ and $(dR/dt)_{mr} = (dR/dt)_{maint}$. For $w < W_\infty$, $(dR/dt)_{mr} > (dR/dt)_{maint}$. The whole trouble comes from developing β as a function of f (equation B1). When β is assumed a constant fraction of the ration as Winberg (1956) does, putting $\beta = 0.8$, then $(dR/dt)_{mr} = (dR/dt)_{maint}$.

A convenient expression for maintenance catabolism is easily derived by allotting a negative sign to the right-hand side of equation B10 and inserting equation B11:

$$-\alpha\left(\frac{dr}{dt}\right)_{maint} - kw^n = -\frac{\alpha kw^n}{1-\alpha} - kw^n = -\frac{kw^n}{1-\alpha}$$

Thus we have:

$$\textit{Maintenance catabolism} = -\frac{kw^n}{1-\alpha} \quad \ldots\ldots(B17)$$

which is proportional with fasting catabolism and independent of β. In equation B17 it is expressed in terms of dissipation of matter, but it may as well be thought of in terms of oxygen consumption by introducing $\omega = dO_2/dw$:

$$\left(\frac{dO_2}{dt}\right)_{maint} = -\frac{\omega}{1-\alpha}kw^n \quad \ldots\ldots(B18).$$

Note that a plot of maintenance oxygen consumption against body weight gives an estimate of n whereas a plot of maintenance ration against body weight does not (equation B13).

We further have:

$$\textit{Growth food} = \frac{dR}{dt} - \left(\frac{dR}{dt}\right)_{mr} = h_1 f w^m - \frac{kw^n}{(1-\alpha)\beta} = \frac{dw/dt}{v} \quad \ldots\ldots(B19)$$

(v is defined below)

Efficiency of utilization of growth food for growth

$$= v = \frac{dw/dt}{d\mathrm{R}/dt - (d\mathrm{R}/dt)_{mr}} = (1-\alpha)\beta \qquad \text{.....(B20)}$$

Efficiency of utilization of total food for growth

$$= u = \frac{dw}{d\mathrm{R}} = -\frac{k}{h_1 f} w^{n-m} \qquad \text{.....(B21).}$$

u and v are dimensionless. Notice that v is independent of body size. v is always positive; u is negative for $dw/dt < 0$.

The maximum utilization of food with respect to feeding level is found by differentiating equation B21 with respect to f, putting $du/df = 0$ and solving for f:

$$f_{\max} = -\frac{h_2}{ln \dfrac{k}{h_1 h_2 (1-\alpha)} + (n-m)\, ln\, w} \qquad \text{.....(B22).}$$

In order to find the total amount of food, R_t, eaten by the fish from its birth until the time t we shall, to facilitate integration, revert to Pütter's approximation (equation 1 or, integrated, equation A28):

$$w_t = \mathrm{W}_\infty (1-e^{-\mathrm{K}t})^3 \qquad \text{.....(A28)}$$

which means putting $m = 2/3$ and $n = 1$. For simplicity, the fish is assumed to be born at time $t = 0$ which puts the initial weight to zero. We have from equation B2

$$d\mathrm{R}/dt = h_1 f w_t^m = h_1 f \mathrm{W}_\infty^m (1-e^{-\mathrm{K}t})^{3m} \qquad \text{.....(B23)}$$

which gives, for constant f,

$$\mathrm{R}_t = h_1 f \mathrm{W}_\infty^m \int_0^t (1-e^{-\mathrm{K}t})^{3m}\, dt \qquad \text{.....(B24).}$$

The integration is simple for $m = 1/3$, $m = 2/3$, and $m = 1$. Results for intermediate values of m can be obtained by interpolation (see discussion below of an analogous situation leading to equation B34).

For $m = 2/3$ equation B24 becomes

$$\mathrm{R}_t = \frac{h_1 f \mathrm{W}_\infty^{2/3}}{2\mathrm{K}} (2\mathrm{K} + (1-e^{-2\mathrm{K}t}) - 4(1-e^{-\mathrm{K}t})) \qquad \text{.....(B25).}$$

The integrated efficiency of utilization of total food for growth becomes

$$U = \frac{\int_o^t \frac{dw}{dt}}{\int_o^t \frac{dR}{dt}} = \frac{w_t}{R_t} = \frac{W_\infty^{1-m}}{h_1 f} \frac{(1-e^{-Kt})^3}{\int_o^t (1-e^{-Kt})^{3m} dt} \quad \ldots\ldots(B26)$$

where the integral can be evaluated as above. Note that Pütter's approximation is used only in the growth curve proper. Other parameters remain as they were.

An equation for maintenance requirements corresponding to equation B23 is similarly derived from equation B16:

$$(dR/dt)_{mr} = \frac{kw^n_t}{v} = \frac{kW^n_\infty}{v} (1-e^{-Kt})^{3n} \quad \ldots\ldots(B27).$$

This, too, is easily integrated to give $R_{t.\,mr}$. The difference $R_t - R_{t.\,mr}$ is the growth food which, by multiplication by v gives the total production of fish meat. These things are perhaps of limited interest because as fish grow some of them usually die. A more realistic model, therefore, incorporates mortality, as suggested below in an approach closely related to that made by Beverton and Holt (1957, paragraph 9.4.3.) who used, however, the Pütter approximation throughout.

For a population with a constant instantaneous mortality, Z, we have

$$N_t = N_o e^{-Zt}$$

where N_t is the number present at time t, and N_o the initial number. Therefore, multiplying equations B23 and B27 by N_t we get

$$_{pop}(dR/dt) = h_1\, f\, w_t^m\, N_t = h_1\, f\, W_\infty^m\, N_o(1-e^{-Kt})^{3m} e^{-Zt}$$

$$_{pop}(dR/dt)_{mr} = \frac{k\, w_t^n N_t}{v} = \frac{k\, W_\infty^{\ n}\, N_o}{v} (1-e^{-Kt})^{3n}\, e^{-Zt}$$

where W_∞ and K, and those only, are Pütter parameters.

Integrated, these equations become, for any constant f,

$$_{pop}R_t = h_1 f\, W_\infty^{\ m} N_o \int_o^t (1-e^{-Kt})^{3m}\, e^{-Zt}\, dt = h_1 f\, W_\infty^{\ m}\, N_o\, J_I \quad \ldots\ldots(B28)$$

$$_{pop}R_{t.\,mr} = \frac{k\, W_\infty^{\ n} N_o}{v} \int_o^t (1-e^{-Kt})^{3n}\, e^{-Zt}\, dt = \frac{k\, W_\infty^{\ n} N_o}{v}\, J_{II} \quad \ldots\ldots(B29)$$

where the integrals J_I and J_{II} are to be evaluated below.

The food utilized for growth up to time t is

$$ {}_{pop}R_{t.g} = {}_{pop}R_{t} - {}_{pop}R_{t.mr} = N_o \left(h_1 f\, W_\infty^m\, J_I - \frac{k\, W_\infty^n}{v}\, J_{II}\right) \quad .....(B30) $$

which, multiplied by v and divided by N_o gives the annual production per fish originally present and still not over t years old:

$$ A.P./N_o = v\, {}_{pop}R_{t.g}/N_o = H\, W_\infty{}^m\, J_I - k\, W_\infty{}^n\, J_{II} \quad .....(B31). $$

Remember, that W_∞ is a Pütter parameter, whereas H and k are not. $H = v\, h_1\, f$ is substituted from equation B9.

Equation B31 can be derived directly from the growth equation without the detour through consumption (see Beverton and Holt, 1957, eq. (9. 19)):

$$ A.P. = \int_o^t (dw/dt)_t\, N_t\, dt = \int_o^t (H\, w^m{}_t - k\, w^n{}_t)\, N_t\, dt $$

$$ = N_o H \int_o^t w^m{}_t\, e^{-Zt}\, dt - N_o k \int_o^t w^n{}_t\, e^{-Zt}\, dt $$

$$ = N_o H\, W_\infty^m\, J_I - N_o k\, W_\infty^n\, J_{II} \quad .....(B31). $$

This way, equation B31 turns out to contain an unnecessary complication: since Pütter's parameters are introduced in the expansion of $w^m{}_t$ and $w^n{}_t$ they might as well be introduced at once. That would be in accordance with our assumption, that the growth curves of most fishes are adequately described by Pütter's approximation. Thus,

$$ A.P. = \int_o^t (dw/dt)_t\, N_t\, dt = \int_o^t (H\, w^{2/3}{}_t - k\, w_t)\, N_t\, dt $$

$$ = N_o\, W_\infty^{2/3}\, H \int_o^t (1-e^{-Kt})^2\, e^{-Zt}\, dt - N_o\, W_\infty\, k \int_o^t (1-e^{-Kt})^3\, e^{-Zt}\, dt $$

and, because $H = k\, W_\infty^{1/3}$ (equation A19),

$$ A.P. = N_o\, {}_1k\, {}_1W_\infty\, (J_{2/3} - J_{3/3}) \quad .....(B32) $$

where suffixes 1 are introduced to indicate that both k and W_∞ are Pütter parameters. Putting

$$ N_o\, {}_1W_\infty^{2/3}\, J_{2/3} = \bar{P}_{w^{2/3}},\ N_o\, {}_1W_\infty\, J_{2/3} = \bar{P}_w \text{ and } {}_1k = 3K \text{ gives} $$

$$ A.P. = 3\, K\, (W_\infty^{1/3}\, \bar{P}_{w^{2/3}} - \bar{P}_w) $$

which is equation (9. 23) of Beverton and Holt (1957) except for the interval over which there was integrated.

The overall efficiency of utilization of total food for growth by the whole population up to time t is

$$_{pop}U_t = A.P./_{pop}R_t \qquad \text{.....(B33)}$$

and can be estimated using either expression for A.P. (see equations B31 and B32). However, since more parameter estimates are involved in equation B31 than in B32 the two estimates of $_{pop}U_t$ are not expected to be identical.

The integrals J_I and J_{II} are easily evaluated for $m = 2/3$ and $n = 1$ which, however, means to extend the use of Pütter's approximation beyond the growth curve proper. The approximation can be avoided by graphical interpolation after evaluating the integral

$$J_x = \int_0^t (1-e^{-Kt})^{3x}\, e^{-Zt}\, dt$$

for $x = \{\, 0, 1/3, 2/3, 1, 4/3 \,\}$:

$$J_0 = \int_0^t (1-e^{-Kt})^0\, e^{-Zt}\, dt = A; \qquad A = \frac{1-e^{-Zt}}{Z}$$

$$J_{1/3} = \int_0^t (1-e^{-Kt})\, e^{-Zt}\, dt = A - B; \qquad B = \frac{1-e^{-(Z+K)t}}{Z+K}$$

$$J_{2/3} = \int_0^t (1-e^{-Kt})^2\, e^{-Zt}\, dt = A - 2B + C; \qquad C = \frac{1-e^{-(Z+2K)t}}{Z+2K}$$

$$J_{3/3} = \int_0^t (1-e^{-Kt})^3\, e^{-Zt}\, dt = A - 3B + 3C - D; \qquad D = \frac{1-e^{-(Z+3K)t}}{Z+3K}$$

$$J_{4/3} = \int_0^t (1-e^{-Kt})^4\, e^{-Zt}\, dt = A - 4B + 6C - 4D + E; \qquad E = \frac{1-e^{-(Z+4K)t}}{Z+4K}$$

.....(B34).

Beverton and Holt (1957) define annual production (A.P.) as the production of only the exploited phase of the population. The same restriction is not made here: annual production can be estimated for any phase (any age interval). All integrations are made between zero time and time t. Integrations from $t = t_1$ to $t = t_2$ are supposed to be made in two stages, from 0 to t_2 and from 0 to t_1, subtracting afterwards the latter from the former. This simplifies each integration which is advantageous if the computations are to be made by means of programmed desk-top calculators or computers. It probably simplifies programming, shortens the program, and reduces the demands for memory.

The parameters of the present paragraph can be estimated from data on growth rate and ration eaten (App. VII). Several may as well be determined from data on ration eaten and oxygen consumption (App. IV).

C. GROWTH AND TEMPERATURE

Several attempts at describing growth or respiration as a function of temperature have been made. Some attacks are clearly empirical, others less so, speaking in vague terms of, e.g. the effect of interaction of enzymes; a rigorous mathematical model based on kinetic forces (Rashevky, 1960) is strictly applicable on the cellular level only. Pütter's (1920) hydraulic analog leads to sensible results but, unfortunately, I cannot quite follow his argument and therefore must refrain from discussing it. A reasoning along chemical lines, however, leads easily to an applicable although perhaps too flexible model.

Assume that metabolic processes in general proceed as described by the Michaelis–Menten equation, i.e. that enzyme, substrate, and water form a complex which under splitting of the water and substrate molecules forms products and free enzyme.

With additional assumptions specified by Casey (1962, p. 203) whose notation is used below, the velocity of the catalyzed process is

$$v_2 = -\frac{d[\mathrm{S}]}{dt} = \frac{k_2[\mathrm{E}]_o\,[\mathrm{S}]_o}{k_{-1}k_1^{-1} + [\mathrm{S}]_o}$$

where brackets denote concentrations in moles or gram per cm^3. E is enzyme and S substrate; the subscript o denotes initial concentrations; k_1 and k_{-1} are the rate constants for forward and backward reactions at the formation of the Michaelis complex, ES; k_2 is the rate at which products are formed; t is time.

Assume also that the velocity of each process involved is a function of activation energy and thus, in solutions, of temperature according to the equation of Arrhenius:

$$k = \mathrm{A}\,\mathrm{e}^{p\tau}$$

where τ is the temperature in centigrades and A is the rate constant for $\tau = 0$.

Then

$$v_2 = -\frac{d[\mathrm{S}]}{dt} = \frac{\mathrm{A}_2\mathrm{e}^{p_2\tau}\;[\mathrm{E}]_o\,[\mathrm{S}]_o}{\mathrm{A}_{-1}\mathrm{e}^{p_{-1}\tau}\;\mathrm{A}_1^{-1}\;\mathrm{e}^{-p_1\tau} + [\mathrm{S}]_o}$$

$$\frac{1}{v_2} = \frac{\mathrm{A}_{-1}}{\mathrm{A}_1\mathrm{A}_2\,[\mathrm{E}]_o\,[\mathrm{S}]_o}\;\mathrm{e}^{(p_{-1}-p_1-p_2)\tau} + \frac{1}{\mathrm{A}_2\,[\mathrm{E}]_o}\;\mathrm{e}^{-p_2\tau}$$

Putting $\frac{1}{\mathrm{A}_2\,[\mathrm{E}]_o} = b$, $\frac{\mathrm{A}_{-1}}{\mathrm{A}_1\,[\mathrm{S}]_o}\,b = a$ and $p_{-1}-p_1-p_2 = p_0$ gives

$$\frac{1}{v_2} = a\mathrm{e}^{p_0\tau} + b\mathrm{e}^{-p_2\tau} \qquad \text{.....(C1)}$$

where a, b, and p_2 are positive, p_o either negative or positive. When concentration is measured in g cm^{-3}, v_2 has the dimension g cm$^{-3}t^{-1}$. Since we are assuming a density of one for the fish body, g and cm^{-3} cancel out and v_2 becomes a rate constant (reciprocal of time). If the growth equation is written in the form

$$\frac{dw}{dt} = \eta w - \kappa w$$

η and κ are, for any fixed value of w, rate constants supposed to behave according to equation C1:

$$\frac{1}{\eta} = {}_{\eta}a\mathrm{e}^{\eta p_0 \tau} + {}_{\eta}b\mathrm{e}^{-\eta p_2 \tau} \qquad \ldots\ldots(\mathrm{C2})$$

$$\frac{1}{\kappa} = {}_{\kappa}a\mathrm{e}^{\kappa p_0 \tau} + {}_{\kappa}b\mathrm{e}^{-\kappa p_2 \tau} \qquad \ldots\ldots(\mathrm{C3}).$$

Substituting in equations C2 and C3 H for η and k for κ is formally wrong (except for Pütter's k in equation (1)). Yet they provide good working approximations with the virtue of depending less (or not at all) upon body size than η and κ. Thus,

$$\frac{1}{\mathrm{H}} = {}_{\mathrm{H}}a\mathrm{e}^{\mathrm{H} p_0 \tau} + {}_{\mathrm{H}}b\mathrm{e}^{-\mathrm{H} p_2 \tau} \qquad \ldots\ldots(\mathrm{C4})$$

$$\frac{1}{k} = {}_{k}a\mathrm{e}^{k p_0 \tau} + {}_{k}b\mathrm{e}^{-k p_2 \tau} \qquad \ldots\ldots(\mathrm{C5}).$$

For applications see App. III and XIII. The applications show that equation C5 may often be further simplified to a single exponential function,

$$k = k_o l^{p_k \tau} \qquad \ldots\ldots(\mathrm{C6})$$

where p_k is positive.

Differentiating equation C1 with respect to τ, putting the derivative equal to zero and solving for τ gives τ_m, the temperature for which v_2 has maximum.

$$\tau_m = \frac{ln\left(\frac{p_2}{p_0}\frac{b}{a}\right)}{p_0 + p_2} \qquad \ldots\ldots(\mathrm{C7}).$$

The maximum exists only for $p_0 > 0$. Taking τ' as an exit instead of 0 C does not vitiate the proportionality with Kelvin degrees and, for $p_0 = p_2 = p$ and $a = b$ reduces equation C1 to

$$\frac{1}{v_2} = \frac{1}{v_2'} \cosh p(\tau - \tau') \qquad \ldots\ldots(\mathrm{C8})$$

which is the catenary curve found empirically by Janisch (1927) to describe the temperature dependence of the growth rate of young animals. It was applied to fishes by Ursin (1963a). The introduction of equation C8 is a trick rather than an approximation because when equation C1 represents a symmetrical curve, a and b usually differ by several size orders. It is a demonstration of the general flexibility of compound exponential functions. The experience warns against putting too much faith into the physiological relevance of parameter values estimated from such curves (Riggs, 1963).

The above results incorporated in equation A19 gives the asymptotic weight as a function of temperature. Thus, using equations C4 and C6 and omitting for simplicity the subscript H:

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} = \left[(ae^{p_0\tau} + be^{-p_2\tau})\, k_o e^{p_k\tau} \right]^{-\frac{1}{n-m}} \qquad \ldots\ldots(C9.)$$

Differentiating with respect to τ, putting $dW_\infty / d\tau = 0$ and solving for τ gives the temperature, $\tau_{\infty m}$, at which the asymptotic weight is maximum:

$$\tau_{\infty m} = \frac{ln \left(\frac{p_2 - p_k}{p_0 - p_k} \frac{b}{a} \right)}{p_0 + p_2} \qquad \ldots\ldots(C10).$$

The maximum exists when

(1) $p_0 < -p_k$ and $p_2 < p_k$

(2) $p_0 > -p_k$ and $p_2 > p_k$

The growth rate as a function of temperature is obtained by inserting equations C4 and C5 into equation B8:

$$\frac{dw}{dt} = (ae^{p_0\tau} + be^{-p_2\tau})^{-1} w^m - k_o\, e^{p_k\tau} w^n \qquad \ldots\ldots(C11).$$

Differentiating $\frac{dw}{dt}$ with respect to τ for constant w and putting the derivative equal to zero leads to the expression

$$k_o p_k e^{p_k \tau_{mg}} w^{n-m} = \frac{p_2 b e^{-p_2 \tau_{mg}} - p_0 a e^{p_0 \tau_{mg}}}{(be^{-p_2 \tau_{mg}} + ae^{p_0 \tau_{mg}})^2} \qquad \ldots\ldots(C12)$$

which can be solved by iteration for τ_{mg}, the temperature at which the growth rate is maximal, for any fixed body size. In one of the limiting cases, $w = 0$, we have $\tau_{mg} = \tau_m$ (equation C7) because, by experience, $n > m$, so that the second right-hand term of equation C11 disappears more rapidly than the first one when $w \rightarrow 0$. At the other limit, $w = W_{\infty m}$ (the value W_∞ attains for $\tau = \tau_{\infty m}$) we have $\tau_{mg} = \tau_{\infty m}$. Application: App. XIII.

D. FASTING CATABOLISM AND OXYGEN SUPPLY

The best clue to the understanding of the relationship between the rate of catabolic processes and the oxygen concentration of the surrounding medium is probably found in Rashevsky's cell model. It has the virtue of being based on phenomena (mainly diffusion and permeability) for which comparatively precise theories are available. In Rashevsky (1960), to which the reader is referred, he has developed a simple model of oxygen supply and oxygen consumption of unicellular organisms, or of individual cells of a multicellular organism.

Let c be the outer oxygen concentration (g cm^{-3}) and Q the rate of oxygen consumption (g cm^{-3} sec^{-1}), with Q* being the asymptotic value of Q, corresponding to $c = \infty$. Then Rashevsky's equation (55) can be written

$$\frac{c}{Q/Q^*} = -\Lambda Q^* + \xi\left(1-\frac{Q}{Q^*}\right)^{-1} \qquad \ldots\ldots(D1)$$

where Q and Q*, being consumptions, are negative. ξ is the concentration of intermediary metabolic products (g cm^{-3}, examplified in the model by lactic acid) and does not particularly interest us here. Λ (sec) is the duration of the oxygen transport through external and internal media and through the cell membrane. Equation D1 is not defined for $Q = Q^*$ in which case, according to Rashevsky's equation (54), Q is independent of Λ. Equation D1 is linear in cQ^*/Q and $(1-Q/Q^*)^{-1}$ so that Λ and ξ can be estimated when Q is known for a range of values of c, some of which are high enough to permit a guess at the asymptote, Q*.

To adapt equation D1 to multicellular organisms is mainly to sum up the oxygen consumptions of individual cells. The organization, however, of such organisms complicates matters because an intermediate medium, the blood, is often introduced between the water and the cell plasma. Λ, therefore, must be redefined to cover the full transport time of oxygen from the water, through the gills, within the blood and through cell membranes and plasma to the exact spot where it is being used. The new Λ has two main components. One is the sum of the Λ,s of individual cells through or into which the oxygen must pass. This first component, Λ_1, is a function of the organizatorial level of the animal and of cell size, but is assumed to be independent of body size. The second component is the transport time for oxygen in the vascular system. The simplest assumption is that it is proportional with length or, because $w = ql^3$, with $w^{1/3}$. Then,

$$\Lambda = \Lambda_1 + \lambda w^{1/3} \qquad \ldots\ldots(D2)$$

where the dimension of λ is sec $g^{-1/3}$. Inserting the foregoing in equation D1 gives

$$\frac{c}{Q/Q^*} = -(\Lambda_1 + \lambda w^{1/3})\,Q^* + \xi\,(1 - \frac{Q}{Q^*})^{-1} \qquad \text{.....(D3).}$$

Thus, when data for oxygen concentration, c, and consumption, Q, are available for a range of body size, separate estimates of Λ_1 and λ can be made by application of equation D2. See App. VI.

Confining ourselves to the study of fasting catabolism we have by means of equation A9

$$\left.\begin{aligned} wQ &= \left(\frac{dO_2}{dt}\right)_{fasting} = \omega\left(\frac{dw}{dt}\right)_{fasting} = -\,\omega\, kw^n \\ Q &= -\,\omega\, kw^{n-1};\ k = -\frac{Q}{\omega}\, w^{1-n} \\ Q^* &= -\,\omega\, k^*\, w^{n-1};\ k^* = -\frac{Q^*}{\omega}\, w^{1-n} \end{aligned}\right\} \qquad \text{.....(D4)}$$

where k^* is the value k attains when $c = \infty$. Equation D4 shows how equation D3 can be applied to data of weight loss during fasting, namely, by the substitution of the rate of weight loss per cm^3 (i.e., per g) for the corresponding rate of oxygen consumption:

$$Q = \frac{\omega}{w}\left(\frac{dw}{dt}\right)_{fasting}.$$

When k is a simple exponential function of temperature,

$$k = k_0 e^{p_k T} \qquad \text{.....(C6)}$$

Λ and Λ_1 are likely to have negative temperature coefficients, because having the dimension of time they can be considered reciprocal rate constants. Even λ, also having time in the denominator of the dimensional expression (sec $g^{-1/3}$), is suspected of having a negative temperature coefficient. Tentatively, therefore,

$$\Lambda = \Lambda_0 e^{p_\Lambda T};\ \Lambda_1 = \Lambda_0\, e^{p_{\Lambda 1} T};\ \lambda = \lambda_0 e^{p_\lambda T} \qquad \text{.....(D5)}$$

where the p's are negative. Again, see App. VI.

E. METABOLIC RATES AND NATURAL MORTALITY

Natural mortality, as usually defined by fishery biologists, is the sum of all causes of mortality except fishing and tagging mortalities. Thus, natural mortality may have both physiological and environmental components. An example of the latter is the activity of predators. Most predators of fish probably are other fish so that the chance of a fish being eaten depends, among other things, upon the number of fish bigger than itself. The reality of a correlation of natural mortality with growth parameters is beyond doubt after the studies of Taylor (1958) and of Beverton and Holt (1959) although uncertainty remains as to which parameter, or parameters, the correlation concerns. Roughly, the situation is that small species have a higher natural mortality rate than big ones. More shall be said on this subject here whereas another aspect of the problem, that of the possibly shorter life-span of small species due to early onset of senility, is passed over.

Since every time a molecular interaction occurs within a cell there must be a chance that something will go wrong, it is not unreasonable to assume that natural mortality as a physiological phenomenon is proportional with the density of molecular interactions in unit time. It can also be assumed that a constant percentage of the cells of the body can be maladjusted at the same time without causing disaster and that, because cell size is usually constant, units of weight can be dealt with instead of number of cells. For the sake of simplicity it shall further be assumed that the number of molecular interactions, and the proportion of faulty interactions, is the same when 1 g of substance is being built up as when it is broken down.

Putting $h_1 f \beta = h$ and dividing the growth equation for the whole fish,

$$dw/dt = h\,w^m - \alpha\,h\,w^m - k\,w^n \qquad \ldots\ldots(\text{B8})$$

by w gives the growth rate per gram:

$$\frac{dw/dt}{w} = h\,w^{m-1} - \alpha\,h\,w^{m-1} - k\,w^{n-1} \qquad \ldots\ldots(\text{E1}).$$

On the assumptions made above, the density of molecular interactions is proportional with the right-hand side of equation E1 when each term is allotted a positive sign. This density, again, should be proportional with the natural mortality to the extent that mortality is a metabolic event. We therefore can put

$$\mathrm{M} = \mu\left((1+\alpha)\,h\,w^{m-1} + k\,w^{n-1}\right)$$

where M is the instantaneous coefficient of natural mortality and μ a dimensionless proportionality constant. Inserting $\mathrm{H} = (1-\alpha)h$ from equation B8 gives

$$\mathrm{M} = \mu\left(\frac{1+\alpha}{1-\alpha}\,\mathrm{H}\,w^{m-1} + k\,w^{n-1}\right) \qquad \ldots\ldots(\text{E2})$$

as applied in App. XII.

Parameter estimates have shown that the second term of equation E2 is probably negligible. Frank approximations led to the rule of thumb,

$$\mathrm{M} \approx w^{-1/3}$$

for species of a size order of $\mathrm{W}_\infty = 10^3$g.

F. LINKING UP WITH WINBERG'S MODEL

One of the major obstacles encountered when comparing mathematical models is a trivial one: that of notation. Differences in notation often obscure important identities or disagreements of basic concepts and underlying assumptions. In order to evaluate the specific merits of each model and decide which can be used with most advantage in the actual situation it is necessary to realize the limitations of applicability of the individual models and the functional relationships between their parameters. There are two recently published models covering more or less the same ground as the one presented. One was described by Winberg in 1956, the other by Paloheimo and Dickie in three papers (1965, 1966a, b). A key to the notation of Winberg's model in terms of the present one is given below, after a discussion of some interesting points. A similar translation of the Paloheimo–Dickie model was intended but not made because it would have been too complicated for practical purposes.

Winberg's growth equation, "the basic balanced equation," is an energy account. It runs (1956, p. 209)

Energy of weight increase + energy of metabolism
= physiologically useful energy
= 0.8 times the energy of the ration

or, in letters (p. 228)

$$\mathrm{P} + \mathrm{T} = 0.8\ \mathrm{R}.$$

The physiologically not useful energy of the food, 0.2 R, is that lost in excrements and urine. The estimate was obtained experimentally as an average for several investigations. A possible dependence upon the feeding level (as assumed by Kostitzin, Ivlev, and myself) is not discussed. The estimated useful fraction, 0.8, is closely related to β which is the fraction absorbed of the food eaten (equation B3). The energy loss through urine is not accounted for specifically in the present model, but is included in α. For most purposes we can, I think, put $0.8\ \mathrm{R} = \beta\ d\mathrm{R}/dt = dr/dt$ where the left-hand term is in Winberg's terminology and the others in mine.

Winberg's energy of metabolism, T, is total catabolism in the other model apart from the fact that one computes in calories, the other in units of weight. T is estimated as the energy equivalent of the oxygen consumption of a comparatively quiet fish, and multiplied by 2 to match the metabolism of the more active, feeding fish. To Winberg, the metabolic level is a function of activity. He does not appreciate feeding catabolism as physiologically distinct from active metabolism. The present paper (following Saunders 1963, see App. IV) recognizes feeding catabolism as a mainly physiological event: the fed fish has a higher metabolic rate than the fasting one, even when at rest. The activity necessitated by feeding is here pushed into the background, being made proportional with the ration taken.

Winberg develops T as a function of body size by means of the so-called "basic equation."

$$\mathrm{Q} = \mathrm{A}\ w^{k}$$

where Q is the rate oxygen consumption in millilitres per hour of a comparatively quiet fish, measured at 20 C. Introducing an expression, C_1, for the conversion of oxygen consumed to calories liberated we have

$$T = 2C_1 Q = 2C_1 A w^k$$

(the symbol C_1 is my own invention). The foregoing is virtually the same as equation A12 in the present paper,

$$dO_2/dt = -D w^d$$

which specifies, however, neither feeding level, nor activity, nor temperature. Converting equation A12 from gram per hour to energy equivalents by multiplying by C_2 we have

$$T \approx C_2 D w^d$$

where D, however, is a function of the feeding level. Writing $C_3\, dw/dt$ for P and $C_3\, \beta\, dR/dt$ for 0.8 R Winberg's balanced equation becomes

$$C_3\, dw/dt = C_3\, \beta\, dR/dt - C_2\, D\, w^d$$

or

$$C_3\, dw/dt = C_3\, dr/dt - C_2\, D\, w^d.$$

C_3 is common to the increment and food terms because we are here assuming that the fish and its food have the same chemical composition (see Introduction) Winberg finds $d \approx 0.8$ which is a good working approximation irrespective of the feeding level. Saunders (see App. IV) found $d = 0.79$ for fed cod and $d = 0.84$ for fasting ones.

Winberg did not develop dr/dt as a function of body size which limits the applicability of the model. However, inserting equation B4 does it:

$$C_3\, dw/dt = C_3\, h\, w^m - C_2\, D\, w^d.$$

In this form and evaluated for some fixed feeding level (e.g. that corresponding to twice the "basic" metabolic level, as Winberg finds it useful to do) "the balanced equation" should be more handy for a purpose for which it has been used: the computation of food or oxygen requirements or of the growth rate of fishes in pond farms. In its original form the equation fails to indicate that the growth rate slows down in old (big) fishes.

The coefficients cannot, unfortunately, be estimated from growth data alone because feeding catabolism, $\alpha\, h\, w^m$ in the present model, in Winberg's is added to the positive term as well as to the negative one and cancels out in studies of growth curves. Partitioning total catabolism into feeding and fasting components we have by means of equation A11

$$T = C_2\, D\, w^d \approx C_2\, (\omega\, \alpha\, h\, w^m - \omega\, k\, w^n) = C_3\, (\alpha\, h\, w^m - k\, w^n).$$

Insertion in Winberg's equation gives

$$C_3\,dw/dt = C_3\,h\,w^m - C_3\,(\alpha\,h\,w^m + k\,w^n) = C_3\,(1-\alpha)\,h\,w^m - C_3\,k\,w^n = C_3\,H\,w^m - C_3\,k\,w^n$$

which apart from the conversion to energy equivalents is identical with equation B8.

Except for the small differences in the underlying assumptions of the two models discussed above, the following key to Winberg's notation can be used:

WINBERG'S NOTATION	NOTATION OF THE PRESENT PAPER
p (cal/time)	dw/dt (weight/time)
T (cal/time)	Total catabolism $= -(h\,w^m + k\,w^n)$; (weight/time)
R (cal/time)	$d\mathrm{R}/dt$ (weight/time)
0.8 (pure number)	β (pure number)
0.8 R (cal/time)	dr/dt (weight/time)
Q (vol/time)	dO_2/dt (weight/time)
A (vol^{1-k}/time)	D (weight^{1-d} /time)
k (pure number)	d (pure number)
$K_1 = 100p/\mathrm{R}$ (pure number)	$100\,u = 100\,dw/d\mathrm{R}$(pure number)
$K_2 = K_1/0.8$ (pure number)	$100\,u/\beta$ (pure number)

SUMMARY AND DISCUSSION

The metabolic model have two fundamental parameters, namely the powers m and n in the equation

$$\frac{dw}{dt} = \mathrm{H}\,w^m - k\,w^n \qquad \text{.....(B8)}$$

upon which further parameter estimation depends. They can be defined as the values making the instantaneous coefficients, H and k, of anabolism and catabolism independent of body weight during the growth of the individual. So many attempts at estimating m and n were made in the Appendixes below that a survey of methods and results is called for. Afterwards, other parameters shall be discussed.

ESTIMATES OF n

There are three entirely independent ways of estimating n: (1) From growth data, inserting simultaneous observations of increment and weight in equation B8 or one of its derivatives (App. X); (2) From the rate of catabolism of fasting fishes. When no food is given the anabolic term of equation B8 is zero. Assuming that the oxygen consumed is used up in catabolic processes we have

$$\frac{dO_2}{dt} = \omega\,\frac{dw}{dt} = -\,\omega\,k\,w^n$$

where $\omega = dO_2/dw$. Using logarithms, n can be estimated as the slope of a straight line when values of weight and either oxygen consumption or weight loss rates are inserted (App. IV, V, and IX). Fed fishes cannot be used because activities of feeding and assimilation are assumed to increase the metabolic rate proportionately, i.e. with w^m, according to the anabolic term of equation B8. Fish fed maintenance ration are an exception (see equation B17). (3) From observations on respiratory surface and body size, assuming that the oxygen consumption of a fasting fish is proportional with respiratory surface (App. XIV).

The estimates made in App. II–XIV are listed in Table I. The figures in parentheses are 95% confidence intervals. There is no obvious disagreement between the results obtained with different methods, so that the model cannot be rejected on this evidence. The interspecific differences are probably not reliable. As a common estimate, $n = 5/6$ seems to be the best guess.

ESTIMATES OF m

There seems to be two ways of estimating m independently of other parameters. 1. Measuring the absorbing surface of the intestine on the assumption that absorption is proportional with the absorbing surface. There are technical difficulties and no reliable estimate is available. 2. Measuring the rate of food consumption in a medium of constant food concentration. This requires the further assumption that food consumption is proportional with absorption, i.e. that the digestion of the ingested food is as efficient in a small specimen as in a big one. Few and rather contradictory data are available.

There are two other methods of estimating m which can be used only when n and k are known. 3. One method is based on the oxygen consumption of fed fishes on the assumption that the extra respiration of fed fishes, as compared with fasting ones, is proportional with the quantity of food absorbed, i.e. with the absorbing surface of the intestine. Thus

$$\left(\frac{dO_2}{dt}\right)_{feeding} = \left(\frac{dO_2}{dt}\right)_{fed} - \left(\frac{dO_2}{dt}\right)_{fasting} \approx -\left(D_w{}^{d} - \omega k w^n\right) = -\,\omega\alpha\, h\, w^m$$

where the proportionality constants do not interest us in this connection. I know of only one investigation of the sort (Saunders, 1963, on cod). 4. The last method is to compute m from growth rate data. Rearranging the growth equation and taking logarithms gives

$$ln\left(\frac{dw}{dt} + k\,w^n\right) = ln\ \mathrm{H} + m\ ln\ w \qquad \ldots\ldots(\mathrm{B8}).$$

The estimate of m is unbiased only when the theoretical values, instead of estimates, of k and n can be inserted.

The estimates made are listed in Table I. They tend to $m < 2/3$. Owing to the many sources of bias it is not yet warranted, however, to reject definitely

TABLE I. Estimates of n, m, and p_k made in various ways in App. II–XIV.

Method of estimation	App. No.	Estimate of n	Estimate of m	Estimate of p_k
Oxygen consumption, many species	II	≥ 0.75		
" " goldfish	III			0.083
" " cod	IV	0.84	0.69	0.060
" " tench	V	0.71		0.084
" " speckled trout	VI			0.090
Food consumption, plaice	VII		0.34; 0.53; 0.65	
Surface of intestine, sole			0.57 (0.33–0.80)	
Weight loss, tench	V			0.096
" " *Lebistes*	VIII			0.071
" " " acclimated	VIII			0.048
" " several species	IX	0.83 (0.78–0.89)		
Growth rates, many species	X	0.83 (0.77–0.89)	for $n = 0.83$: 0.59 (0.56–0.61)	
" " *Lebistes*	XIII		for $n = 1$: 0.50 (0.42–0.58)	0.085
Respiratory surface, *Micropterus*	XIV	< 0.78		
" " many species	XIV	< 0.83		
" " *Zoarces*, eel	XIV	0.83		

the hypothesis of isometric growth (i.e. $m = 2/3$) involved in Pütter's original model. The low value ($m = 0.50$) for *Lebistes*, a very small fish, raises a suspicion that m may be a function of asymptotic size. An increase of m from 0.50 in the smallest species to 0.67 in the biggest ones would not be at variance with the findings in App. X.

The present knowledge of m is not as precise as that of n although it is good enough for most practical purposes. Even the original model, with $n = 1$ and $m = 2/3$, is still the best approach in many cases, particularly because it is easily integrated and describes nicely the growth curves of most fishes. It should probably not be abandoned except when the line of reasoning makes it necessary to use more accurate estimates of the parameters, particularly in metabolic studies.

It is remarkable how well the Pütter approximation has worked in the extensive model developed by Beverton and Holt (1957). Through over 400 pages of text there is only one situation, as far as I can see, where the approximation would lead to obvious disaster. It is in the case of estimating the maintenance ration as a function of body size (p. 301). According to the model the maintenance ration should be almost proportional with the catabolic rate ($-kw$) with reversed sign and, thus, with body weight. That, however, is a hypothesis which can easily be rejected. Beverton and Holt avoid the trouble by introducing an empirical relationship, ζw^j. By an unfortunate choice of experimental data they are led to the belief that $j = 2/3$, whereas $j = n = 5/6$ would have been more appropriate. With this small amendment the Beverton–Holt model remains unrejected as far as it goes, because separate estimation of catabolic parameters was not attempted elsewhere, except for casual references to a paper by von Bertalanffy in which some misconceptions had crept in.

ESTIMATES OF H AND k

The equation for asymptotic size

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad \ldots\ldots(A19)$$

shows that one or several of the four fundamental parameters of the growth equation are functions of asymptotic size, i.e. of the size of the species. There is plenty of evidence (App. II) that with few exceptions n is practically constant throughout the animal kingdom, and in App. IX it was found that the coefficient of fasting catabolism, k, is independent of asymptotic size in fishes. Thus, either H or m, or both, must depend upon asymptotic size. Assuming m constant it was found in App. X that at about 10 C the mean value of H varies (in units of $g^{0.44}$ years^{-1}) from 1 in small species to 40 in big ones. At the same temperature k was found to be about 2.5 $g^{1/6}$ years^{-1} as an average for 81 fish species. The obscure dimensional relations are introduced with the exponential functions H w^m and $k\ w^n$ in the growth model. One of several advantages of Pütter's simple model:

$$\frac{dw}{dt} = \mathrm{H}\ w^{2/3} - k\ w \quad \text{or} \quad \frac{dl}{dt} = \mathrm{E} - \mathrm{K}\ l \qquad \text{.....(A23)}$$

is that the coefficients have the simple physical dimensions of rate and speed.

The variation of k with temperature was investigated for several species (App. III–VI, VIII, and XIII) and that of H for *Lebistes* (App. XIII). k increases almost exponentially with temperature. The temperature coefficient, p_k of equation C6: $k = k_0\ e^{p_k\tau}$ was estimated in several ways, and the results listed in Table I.

The average of the eight available estimates is $p_k = 0.78$ which means that a temperature increase of 10 C causes k to increase by a factor 2.2 or approximately, what one would expect in a simple chemical process. The two estimates for *Lebistes*, acclimated since birth to the experimental temperature are interesting because Stroganov (1956) found that fish respiration is less dependent on temperature in the vicinity of the temperature to which the fish is accustomed. Accordingly, the estimate from weight loss data (p_k = 0.048) is definitely on the low side. That from growth data (p_k = 0.085) over the same temperature range, however, is not. Winberg (1956) doubts the validity of Stroganov's conclusions and points out that even if reliable they would not necessarily lead to a reduced temperature coefficient over a wide range of temperature.

The exponential approximation,

$$k = k_0\ e^{p_k\tau} \qquad \text{.....(C6)}$$

is not sufficiently good when a wide temperature interval is investigated, as for instance in App. III (28 C). In such cases it is necessary to return to the theoretically better founded approximation.

$$\frac{1}{k} = a\ e^{p_0\tau} + b\ e^{-p_2\tau} \qquad \text{.....(C5)}$$

which describes adequately the respiration of Krogh's famous goldfish as a function of temperature (App. III). Anabolic processes, as indicated by the instantaneous coefficient H, seem to have a definite temperature maximum. This was found in the single case investigated here (App. XIII) and is confirmed by previous work (Ursin 1963a, b). The model describes the variations adequately by means of a sum of two exponentials.

A hypothesis on the influence of the oxygen concentration in the surrounding medium is presented in what is probably the most airy part of the model. The duration of oxygen transport in the body (through tissues and in the vascular system) is involved and is estimated indirectly in

App. VI. The obvious way to reject the hypothesis is to obtain somehow a direct measurement of the duration of oxygen transport and compare with the estimates obtained by indirect methods. These indicated that the average time needed by an oxygen molecule to travel from a situation immediately outside the gill surface to the exact spot where it is being used is of the size order 10^2 sec. The choice of the speckled trout, *Salvelinus fontinalis*, for the computations in App. VI is probably a lucky one although it was made merely because good data were available. The respiration of *Salvelinus* is unimpeded only at oxygen concentrations above the saturation point of water, and the effects of oxygen concentration upon the catabolic processes can be followed over a wide range of concentration. In many other species the respiration seems to be practically maximum at an oxygen concentration slightly over the asphyxiation level, as can be seen from data compiled by Winberg (1956).

The model of the influence of feeding upon growth is closely related to that presented by Beverton and Holt (1957). In the present model, however, the partitioning of total catabolism into fasting catabolism ($-k\ w^n$ in the growth equation) and feeding catabolism ($-\ \alpha\ h\ w^m$), the latter proportional with anabolism, is more complete. We have

$$\frac{dw}{dt} = h\ w^m - (k\ w^n + \alpha\ h\ w^m) = \mathrm{H}\ w^m - k\ w^n \qquad \ldots\ldots(\mathrm{B8}).$$

This formulation seems to have led to more adequate concepts of efficiency of food conversion as a function of time and size (equations B20, B21, and B26).

The same formulation is used in a model of natural mortality as a metabolic event. It is assumed that each molecular reaction has an equal chance to go wrong, with the risk of killing the fish. Assuming further, that the number of molecular reactions performed is proportional with the sum of the weights of material built up and material broken down, leads to a hypothesis (equation E2) implying that small species have the highest mortalities. This is in accordance with experience, but it is not quite obvious how, if wrong, the basic concepts of the hypothesis (mortality introduced with molecular interactions) can be rejected by direct observation.

ACKNOWLEDGMENTS

I am greatly indebted to Mr Harry Knudsen, who read the entire manuscript, and to Mr K. P. Andersen who read the theoretical part of it. They discovered several blunders which I should have been most unhappy about if they had been published.

REFERENCES

AHMAN, G., AND G. JØRGENSEN. 1964. Fodermidlernes kemiske sammensaetning og naeringsindhold. Dansk Pelsdyravl, No. 7.

BAGENAL, T. B. 1954. The growth rate of the hake *Merluccius merluccius* (1.) in the Clyde and other Scottish sea areas. J. Marine Biol. Assoc. U.K., **33**: 69–95.

1955. The growth rate of the long rough dab *Hippoglossoides platessoides* (Fabr.). Ibid., **34**: 297–311 and **34**: 643–647.

BAXTER, JOHN L., ET AL. 1960. A study of the yellowtail (*Seriola dorsalis*). State Calif. Dept. Nat. Resources, Div. Fish. Game, Fish Bull., **110**: 1–96.

BERTALANFFY, VON, L. 1934. Untersuchungen über die Gesetzlichkeit des Wachstums I. Roux' Arch., **131**: 613–653.
1938. A quantitative theory of organic growth. Human Biol., **10**: 181–213.
1951. Theoretische Biologie. 2nd ed. A. Francke, Bern.
1964. Basic concepts in quantitative biology of metabolism. Helgolaender Wiss. Meeresuntersuch, **9**: 5–34.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Min. Agr. Fish. Food, Fish. Invest. Ser. 2, **19**: 1–533.
1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Found. Coll. Ageing, **5**: 142–180.

BOUGIS, P. 1952. La croissance des poissons Méditerranéens. Vie Milieu, Suppl. No. 2.

BOWERS, A. B. 1959. Growth of the witch (*Glyptocephalus cynoglossus* (L.)) in the Irish Sea. J. Conseil Conseil Perm. Intern. Exploration Mer, **25**: 168–176.

BRODY, S. 1945. Bioenergetics and growth. Reinhold, New York. 1023 p.

BÜCKMANN, A. 1952. Vorläufige Mitteilung über Fütterungs- und Wachstumsversuche mit Schollen im Aquarium. Kurze Mitt. Fishereibiol. Abt. Max-Planck-Inst., No. 1: 8–20.

CARLISLE, J. G., J. W. SCOTT, AND N. J. ABRAMSON. 1960. The barred surfperch (*Amphisticus argenteus* Agassiz) in Southern California. State Calif. Dept. Nat. Resources, Div. Fish Game, Fish. Bull., **109**: 1–79.

CASEY, E. J. 1962. Biophysics. Concepts and mechanisms. Reinhold Publishing Corporation, New York. 335 p.

CLARK, F. N. 1925. The life history of *Leuresthes tenuis*, an atherine fish with tide controlled spawning habits. State Calif. Fish. Game Comm. Fish. Bull., **10**: 1–51.

CHANG, H. W. 1951. Age and growth of *Callionymus lyra* L. J. Marine Biol. Assoc. U.K., **30**: 281–296.

CHATWIN, B. M. 1958. Mortality rates and estimates of theoretical yield in relation to minimum commercial size of lingcod (*Ophiodon elongatus*) from the Strait of Georgia, British Columbia. J. Fish. Res. Bd. Canada, **15**(5): 831–849.

DAWES, B. 1930. Growth and maintenance in the plaice (*Pleuronectes platessa* L.) Part I. J. Marine Biol. Assoc. U.K. (N.S.), **17**: 103–174.
1931. Growth and maintenance in the plaice (*Pleuronectes platessa* L.) Part II. Ibid., **17**: 877–975.

EGE, R., AND A. KROGH. 1914. On the relation between the temperature and the respiratory exchange in fishes. Intern. Rev. Ges. Hydrobiol. Hydrog., **7**: 48–55.

FOOD AND AGRICULTURE ORGANIZATION. 1960. Proceedings of the world scientific meeting on the biology of sardines and related species. No. 2. Rome.
1963. Proceedings of the world scientific meeting on the biology of tunas and related species. FAO Fish. Rept. No. 6. Vol. 2.

FITCH, JOHN E. 1951. Age composition of the southern California catch of Pacific mackerel 1939–40 through 1950–51. State Calif. Dept. Nat. Resources, Div. Fish Game, Fish Bull., **83**: 1–73.

FRANCA, DA, PEDRO. 1953. Determinaçao da idade em *Gambusia holbrookii* (Girard). Arquiv. Museum Bocage, Lisboa, No. 24.

FROST, W. E., AND CH. KIPLING. 1959. The determination of the age and growth of pike (*Esox lucius* L.) from scales and opercular bones. J. Conseil Conseil Perm. Intern. Exploration Mer, **24**: 314–341.

FRY, F. E. J. 1957. The aquatic respiration of fish. *In* M. E. Brown [ed.] Physiology of fishes. Vol. 1. p. 1–63.

GRAVIER, R. 1961. Les bars (loups) du Maroc atlantique, *Morone labrax* (L.) et *Morone punctata* (Block). Rev. Trav. Inst. Pêches Marine, **25**: 281–292.

GRAY, I. E. 1953. The relation of body weight to body surface area in marine fishes. Biol. Bull., **105**: 285–288.
1954. Comparative study of the gill area of marine fishes. Ibid., **107**: 219–225.

HAGERMAN, F. B. 1952. The biology of the Dover sole, *Microstomus pacificus* (Lockington). State Calif. Dept. Nat. Resources, Div. Fish Game, Fish Bull., **85**: 1–48.

HALD, A. 1952. Statistical theory with engineering applications. Wiley Publications, New York. 783 p.

HEMMINGSEN, A. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rept. Steno Mem. Hosp., **9**(2): 1–110.

HEWSON, L. C. 1955. Age, maturity, spawning and food of the burbot, *Lota lota*, in Lake Winnipeg. J. Fish. Res. Bd. Canada, **12**(6): 930–940.

HODGSON, W. C. 1925. Investigations into the age, length and maturity of the herring of the southern North Sea. Fish. Invest. Ser. **2**, **7**(8): 1–36.

ILES, T. D., AND P. O. JOHNSON. 1962. The correlation table analysis of a sprat (*Clupea sprattus* L.) yearclass to separate two groups differing in growth characteristics. J. Conseil Conseil Perm. Intern. Exploration Mer, **27**: 287–303.

IVLEV, V. S. 1961a. [On the utilization of food by plankton-eating fishes.] Tr. Sevasttopol'sk. Biol. St. Akad. Nauk SSSR, **14**: 188–201. (Fish. Res. Bd. Canada Transl. Ser. No. 447).
1961b. [Experimental ecology of the feeding of fishes.] (Transl. from Russian.) 302 p. Yale University Press, New Haven, Conn.

JANISCH, E. 1927. Das Exponentialgesetz als Grundlage einer vergleichenden Biologie. Abhandl. Z. Theorie Org. Entwicklungsmech., **2**: 1–371.

JOB, S. V. 1955. The oxygen consumption of *Salvelinus fontinalis*. Univ. Toronto Studies, Biol. Ser., No. 61, Publ. Ont. Fish. Res. Lab., No. 73. 39 p.

JONES, J. W. 1953. Age and growth of the trout, grayling, perch, and roach of Llyn Tegid (Bala) and roach in the river Birket. Fish. Invest. Ser. 1, **5**(7): 1–18.

JONES, J. W., AND H. B. N. HYNES. 1950. The age and growth of *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Spinachia vulgaris* as shown by their otoliths. J. Animal Ecol., **19**: 59–73.

JOSEPH, D. C. 1962. Growth characteristics of two southern California surffishes the California corbina and spotfin croaker, family Sciaenidae. Res. Agr. Calif., Dept. Fish Game, Fish Bull., **119**: 1–54.

KÄNDLER, R. 1949. Über den Steinbutt der Ostsee. Ber. Deut. Wiss. Komm. Meeresf., **11**: 73–136.

KÄNDLER, R., AND FR. THUROW. 1959. On the stock of flatfish and cod and the yields of the German fishery in the Baltic. Rappt. Procès-Verbaux Réunions Conseil Perm. Intern. Exploration Mer, **147**: 24–38.

KESTNER, O., AND R. PLAUT. 1924. Physiologie des Stoffwechsels. Handbuch Vergleichenden Physiol., **2**(2): 901–1112.

KETCHEN, K. S. 1961. Observations on the ecology of the Pacific cod (*Gadus macrocephalus*) in Canadian waters. J. Fish. Res. Bd. Canada, **18**(4): 513–558.

KNAUTHE, K. 1897. Untersuchungen uber Verdauung und Stoffwechsel der Fische. I. Z. Fischerei Bd., **5**: 189.
1898. Untersuchungen uber Verdauung und Stoffwechsel der Fische. II. Z. Fischerei Bd., **6**: 139.

KOHLER, A. C. 1964. Variations in growth of Atlantic cod (*Gadus morhua* L.). J. Fish. Res. Bd. Canada, **21**(1): 57–100.

KOSTITZIN, V. A. 1937. Biologie mathematique. Paris.

KROGH, A. 1904. Some experiments on the cutaneous respiration of vertebrate animals. Skand. Arch. Physiol., **16**: 348–357.
1916. The respiratory exchange of animals and man. London.

LINDSTEDT, PH. 1914. Untersuchgen uber Respiration und Stoffwechsel von Kaltblütern. Z. Fischerei., **14**: 193.

LIPSCHÜTZ, A. 1911. Über den Hungerstoffwechsel der Fische. Z. Allgem. Physiol., **12**: 118.

MATSUURA, S. 1961. Age and growth of flatfish, Ganzo-birame, *Pseudorhombus cinnamoneus* (Temm. et Schl.). Rec. Oceanog. Works Japan (Spec. No. 5): 103–110.

MESSTORFF, J. 1959. Untersuchungen über die Biologie des Wittlings, *Merlangius merlangus* (L), in der Nordsee. Ber. Deut. Wiss. Komm. Meeresf., **15**(4): 277–334.

MILLER, P. J. 1961. Age, growth and reproduction of the rock goby, *Gobius paganellus* L., in the Isle of Man. J. Marine Biol. Assoc. U.K., **41**: 757–769.

MIO, SHIN-ICHI. 1960a. Biology of *Sebasticus marmoratus* Cuv. et Val. Rec. Oceanog. Works Japan, **5**(2): 77–85.

1960b. Biology of *Sebastes inermis* Cuv. et Val. Ibid., **5**(2): 86–93.

1961. Age and growth of red sea bream, *Evynnis japonica* Tanaka. Ibid., (Spec. No. 5): 95–101.

MOTODA, S. 1963. Review of Japanese herring investigations. Rappt. Procès-Verbaux Réunions Conseil Perm. Intern. Exploration Mer, **154**: 249–261.

MUIR, B. S. 1960. Comparison of growth rates for native and hatchery-stocked populations of *Esox masquinongy* in Nogies Creek, Ontario. J. Fish. Res. Bd. Canada, **17**(6): 919–927.

NAWRATIL, O. 1961. The pilchard of South West Africa. Admin. S.-W. Africa Marine Res. Lab. Invest. Rept. No. 2.

NÉDÉLEC, C. 1958. Biologie et pêche du maquereau. Rev. Trav. Inst. Pêche Marine, **22**: 121–134.

O'CONNELL, CH. P. 1953. The life history of the cabezon *Scorpaenichthys marmoratus* (Ayres). State Calif. Dept. Nat. Resources, Div. Fish Game, Fish. Bull., **93**: 1–76.

ORCUTT, H. G. 1950. The life history of the starry flounder, *Platichthys stellatus* (Pallas). Ibid., **78**: 1–64.

PALOHEIMO, J. E., AND L. M. DICKIE. 1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Bd. Canada, **22**(2): 521–542.

1966a. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. Ibid., **23**(6): 869–908.

1966b. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. Ibid., **23**(8): 1209–1248.

PETERSEN, C. G. J. 1922. Om rødspaettebestanden og rødspaettefiskeriet i forskellige vande. Ber. Dan. Biol. Stat., **29**: 1–40.

PHILLIPS, J. B. 1948. Growth of the sardine, *Sardinops coerulea*, 1941–42 through 1946–47. State Calif. Dept. Nat. Resources, Div. Fish Game, Fish Bull., **71**: 1–32.

PITT, T. K. 1958. Age and growth of the capelin, *Mallotus villosus* (Muller) from Newfoundland and Grand Bank areas. J. Fish. Res. Bd. Canada, **15**(3): 295–311.

PRICE, J. W. 1931. Growth and gill development in the smallmouthed black bass, *Micropterus dolomieu*, Lacépède. Ohio State Univ. Studies, **4**: 46 p.

PRUTER, A. T. 1954. Age and growth of the Oregon sablefish, *Anoplopoma fimbria*. Pacific Marine Fish. Comm. Portland, Oregon, Bull., **3**: 121–128.

PRUTER, A. T., AND D. L. ALVERSON. 1962. Abundance, distribution, and growth of flounders in the southeastern Chukchi Sea. J. Conseil Conseil Perm. Intern. Exploration Mer, **27**(1): 81–99.

PÜTTER, A. 1920. Studien über physiologische Ähnlichkeit. VI. Wachstumsähnlichkeiten. Pflügers Arch. Ges. Physiol., **180**: 298–340.

RAE, B. B. 1948. Lemon soles at Iceland 1924–39, with special reference to Faxa Bay. J. Conseil Conseil Perm. Intern. Exploration Mer, **15**: 295–317.

1951. A comparison of the pre-war and post-war stocks of lemon soles at Faroe. Ibid., **17**: 242–260.

RASHEVSKY, N. 1959. Some remarks on the mathematical theory of nutrition of fishes. Bull. Math. Biophys., **21**: 161–183.

1960. Mathematical biophysics. Vol. 1. 3rd ed. Dover Publications, New York. p. 1–488.

REUSS, H., AND E. WEINLAND. 1912. Über die chemische Zusammensetzung der Aalbrut unter verschiedenen Bedingungen. Z. Biol., **59**: 283.

RIGGS, D. S. 1963. The mathematical approach to physiological problems. The Williams and Wilkins Co., Baltimore, Md. 445 p.

SAEMUNDSSON, B. 1923. On the age and growth of the cod (*Gadus callarias*) in Icelandic waters. Medd. Komm. Havunders Ser. Fiskeri, **7**(3): 1–35.

SAUNDERS, R. L. 1963. Respiration of the Atlantic cod. J. Fish. Res. Bd. Canada, **20**(2): 373–386.

SCOFIELD, E. C. 1931. The striped bass of California (*Roccus lineatus*). State Calif. Dept. Nat. Resources, Div. Fish Game, Fish Bull., **29**: 1–82.

SHIOKAWA, T. 1962. Studies on habits of coastal fish in the Amakusa islands. Part 2. Growth and maturity of the purple rockfish, *Sebastes p. pachycephalus* (Temm. et Schl.). Rec. Oceanog. Works Japan (Spec. No. 6): 103–111.

SIGURDSSON, A. 1956. Contribution to the life history of the halibut at the west of Iceland in recent years (1936–1950). Medd. Danm. Fiskeri-og Havunders (N.S.), **1**(16): 1–24.

SOUTHWARD, G. M. 1962. A method of calculating body lengths from otolith measurements for Pacific halibut and its application to Portlock-Albatross grounds data between 1955 and 1957. J. Fish. Res. Bd. Canada, **19**(2): 339–362.

STEELE, D. H. 1963. Pollack (*Pollachius virens* (L.)) in the Bay of Fundy. Ibid., **20**(5): 1267–1314.

STROGANOV, N. S. 1956. [Physiological adaptability of fish to the temperature of the surrounding medium.] (Transl. from Russian, Washington, 1962.)

TÅNING, Å. V. 1948. The plaice in Faxa Bay. Rappt. Procès-Verbaux Réunions Conseil Perm. Intern. Exploration Mer, **120**: 39–45.

TAYLOR, CLYDE C. 1958. Cod growth and temperature. J. Conseil Conseil Perm. Intern. Exploration Mer, **23**(3): 366–370.

1962. Growth equations with metabolic parameters. Ibid., **27**: 270–286.

TIEWS, KL. 1957. Biologische Untersuchungen am Roten Thun (*Thunnis thynnus* (L.)) in der Nordsee. Ber. Deut. Wiss. Komm. Meeresf., **14**(3): 192–220.

TSUKAHARA, H. 1962. Biology of the cutlassfish, *Trichiurus lepturus* L. Rec. Oceanog. Works Japan (Spec. No. 6): 57–64.

URSIN, E. 1963a. On the incorporation of temperature in the von Bertalanffy growth equation. Medd. Danm. Fiskeri-og Havunders (N.S.), **4**: 1–16.

1963b. On the seasonal variation of growth rate and growth parameters in Norway Pout (*Gadus esmarki*) in the Skagerrak. Ibid., **4**: 17–29.

WALFORD, L. A. 1932. The California barracuda (*Sphyraena argentea*). State Calif. Dept. Nat. Resources, Div. Fish Game, Fish Bull., **37**: 1–120.

WHITNEY, R. R. 1961a. The bairdiella, *Bairdiella icistius* (Jordan and Gilbert). Ibid., **113**: 105–164.

1961b. The orangemouth corvina, *Cynoscion xanthulus* (Jordan and Gilbert). Ibid., **113**: 165–183.

WINBERG, G. G. 1956. [Rate of metabolism and food requirements of fishes.] Nauchn. Tr. Belorussk. Gos. Univ. Lenina, Minsk. 253 p. (Fish. Res. Bd. Canada, Transl. Ser. No. 194.)

1961. [New information on metabolic rate in fishes.] Vopr. Ikhtiol., 1, **1**(18): 157–165. (Fish. Res. Bd. Canada, Transl. Ser. No. 362.)

1962. [The energy principle in studying food associations and the productivity of ecological systems.] Zool. Zh., **41**(11): 1618–1630. (Fish. Res. Bd. Canada, Transl. Ser. No. 433.)

YOUNG, P. H. 1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947–58. Res. Agr. Calif. Dept. Fish Game, Fish Bull., **122**: 1–67.

YUNOKAWA, Y. 1961. On the age and growth of *Chelidonichthys kumu* (Lesson et Garnot). Rec. Oceanog. Works Japan (Spec. No. 5): 111–116.

ZEMSKAJA, K. A. 1959. Characteristics of the fishing stock of flounder in the central Baltic. Rappt. Procès-Verbaux Réunions Conseil Perm. Intern. Exploration Mer, **147**: 73–74.

APPENDIXES

The examples below (App. II–XIV) are selected in such a way that, as far as possible, they indicate different ways of estimating the same parameter. Of particular interest is to obtain estimates of the same parameter from both respiration and growth data because the limitations of the applicability of the model can be expected to come out clearly that way. This, however, has not been possible with all parameters.

It was attempted to keep each example independent of the others. This, however, could not be accomplished because it was often necessary to "borrow" a parameter estimate from another example. Particularly, App. X, XI, and XII are closely linked by parameter estimates, and so are App. VIII and XIII.

Under each caption are listed the parameters estimated in that paragraph. An index of the notation adopted is given as App. I. It includes references to parameter estimates in the examples. A discussion of methods and results of parameter estimations is found above.

Many linear regression analyses, by the method of least squares, have been made regardless of the fact that the independent variable varies stochastically. This means that the slopes are more or less underestimated throughout.

APP. I. NOTATION

Most of the symbols used are defined below. Some of those omitted are of restricted use in the paragraphs "Growth and Food" or "Growth and Temperature" and do not appear in the final equations. Others are auxiliary parameters introduced occasionally in the Appendixes. Some letters from the standard notation of mathematical statistics have been used without, I hope, great risk of confusion with the parameter notation.

After each definition is added, in parentheses, the serial number of the equation in which the letter in question is introduced. The parenthesis is followed by the serial numbers of Appendixes in which estimates are made. A following expression, in brackets, indicates the dimension of the quantity in terms of W, weight; L, length; T, time; and C, temperature. Empty brackets indicate a pure number. Thus, e.g. B7 IV, VII [$W^{1/3}T^{-1}$] means that the parameter in question is introduced in equation B7, estimated in App. IV and VII, and expressed in terms of cube root of weight per unit time. The frequent use of empirical approximations lends non-physical dimensions to many quantities, e.g. powers of length other than 1, 2, or 3. Sometimes, the dimension of one parameter depends on the value of another.

Finally, the corresponding letter in the notation of Beverton and Holt (1957) is stated when the identity of the parameters is obvious, except for slight differences in the underlying assumptions.

LATIN LETTERS

A_b	Proportionality constant relating body area to body weight. A6 XIV [L^2 $W^{-2/3}$]
A_g	Proportionality constant relating gill area to body weight. A6 XIV [L^2 W^{-n_g}]
a b	Constants entering the expression for the velocity of enzymatic processes as a function of temperature. With suffixes indicating the group of processes (e.g. anabolic) concerned. C1–C5 III, XIII [Dimensions as v_i^{-1}]
B_b	Rate of oxygen consumption through the skin, in unit time and area. A7 [W L^{-2} T^{-1}]
B_g	Rate of oxygen consumption through the gills, in unit time and area. A7 [W L^{-2} T^{-1}]
C	Designates various arbitrary constants.
c	Oxygen concentration of the outer medium. D1 [W L^{-3}]
D	The instantaneous coefficient of oxygen consumption, disregarding the feeding condition of the fish. A12 II, IV [W^{1-d} T^{-1}]
d	The power of weight with which the rate of oxygen consumption is proportional, disregarding the feeding condition of the fish. A12 II, IV [ ]

E	The instantaneous coefficient of anabolism in the equation of growth in length ($E = H/(3q^{1-m})$). A18 XIII [$L^{3(1-m)}$ T^{-1}]. E
e	The base of natural logarithms. [ ]
f	The feeding level, i.e. the fraction of maximum food consumption practised. B1 VII [ ]
f_{maint}	The value of f corresponding to maintenance ration. B14 VII [ ]
f_{max}	The value of f ensuring maximum utilization of food for growth. B22 VII [ ]
H	The instantaneous coefficient of net anabolism. (Suffixes ($_1H$ and $_nH$) indicate differences caused by the choice of values of other parameters.) 1 VII, X, XI, XII [W^{1-m} T^{-1}]. H
h	The instantaneous coefficient of gross anabolism. B4 [W^{1-m} T^{-1}]
h_1	Another instantaneous coefficient of gross anabolism, made independent of rate of food consumption and of fraction absorbed. A2 VII [W^{1-m} T^{-1}]
h_2	An arbitrary constant entering the expression for fraction food absorbed, β. B3 VII [ ]
J_x	An integral, further specified by some suffix. B28 VII [ ]. $\overline{P}_w\, x / R\, W_\infty^{2/3}$
K	The instantaneous coefficient of catabolism in the equation of growth in length ($K = k/(3\, q^{1-n})$). A18 XII [$L^{3(1-n)}$ T^{-1}]. K
k	The instantaneous coefficient of fasting catabolism. (Suffixes ($_1k$ and $_nk$) indicate differences caused by the choice of values of other parameters) 1 III, IV, VII, VIII, IX, X, XI, XIII [W^{1-n} T^{-1}]. k
k_0	k at 0 C. C6 III, V, VIII
k^*	The value of k when the outer oxygen concentration is infinite. D4
L_∞	Asymptotic length. A20 XIII [L]. L_∞
L_I	Length at point of inflection of the curve of growth in length. A21 [L]
l	Body length as a variable. [L]. l
l_t	Body length as a function of time. A27 [L]. l_t
M	The instantaneous coefficient of natural mortality. E2 XII [T^{-1}]. M
m	The power of weight with which the rate of anabolism is proportional. A2 IV, VII, X, XIII [ ]. n
N_t	The number of fish in a population at time t. [ ]. N_t
N_0	The initial number. [ ]
N_r	The number of recruits at time t_r. [ ]. R
n	The power of weight with which the rate of fasting catabolism is proportional. A8 IV, V, IX, X, XIV [ ]. m and j
n_g	Power of body weight with which gill area is proportional. A6 XIV [ ]
p p_0 p_2	Temperature coefficients of processes. Suffixes indicate the group of processes (e.g. anabolic) concerned. C1–C6, D5 III, IV, V, VI, VIII, XIII [C^{-1}]
pop	As a suffix distinguishes population parameters, accounting for mortality. B28
Q	Rate of oxygen consumption per unit body volume (or, because $w = ql^3$, per unit body weight). D1 [W L^{-3} T^{-1}] or [T^{-1}]
Q^*	The value of Q for infinitely high oxygen concentrations in the outer medium. D1
q	Proportionality factor relating body weight to body length. [W L^{-3}]. q
q'	Proportionality factor relating body surface to body length. [ ]. p
R	Weight of food consumed. A1 [W]. ξ

R_t	Food consumed up to time t. B24 VII [W]. ξ
r	Weight of food absorbed. [W]
S_b	Body surface area excluding gills. A6 XIV [L^2]
S_g	Gill surface area. A6 XIV [L^2]
t	Time. 1 [T]. t
t_0	The time when the length of the fish is zero (the alleged birthday). A27 [T]. t_0
t_r	The age at recruitment counted from the moment when $t = 0$. [T]. t_ρ
${}_0t_r$	$= t_0 + t_r$: the age at recruitment counted from the alleged birthday, t_0. VII [T]
U	Effiency of utilization of total food up to time t. B26 VII [ ]
u	Efficiency of utilization of total food for growth, i.e. the fraction of total food actually appearing as growth. B21 VII [ ]
v	Efficiency of utilization of growth food for growth, i.e. the fraction of growth food actually appearing as growth. B20 VII [ ]. ϵ
v_2	Velocity of an enzymatic process. C1 [$W\ L^{-3}\ T^{-1}$] or [$L^{-3}\ T^{-1}$] or [T^{-1}]
W_∞	Asymptotic weight (suffixes (${}_1W_\infty$, ${}_nW_\infty$) indicate differences caused by the choice of other parameters). A19 VII, X, XI, XIII [W]. W_∞
$W_{\infty m}$	The maximum value of asymptotic weight as a function of temperature. See τ_{mg} [W]
W_I	Weight at point of inflection of the curve of growth in weight. A22 [W]
w	Body weight as a variable. [W]. w
w_t	Body weight as a function of time. (w_0, weight at time zero, etc.). A13 [W]. w_t
$\hat{w}$	Approximate mean weight of fish used in the estimation of a growth curve. (9–3) X, XII [W]
Z	The instantaneous coefficient of total mortality. B28 [T^{-1}]

Greek Letters

α	The fraction of gross anabolism spent on feeding catabolism. A3 VII [ ]
β	Fraction absorbed of food eaten. [ ]
β_{maint}	Fraction absorbed of maintenance ration. B12 VII [ ]
η	Proper rate constant of anabolism. C2 [T^{-1}]
κ	Proper rate constant of catabolism. C3 [T^{-1}]. k
Λ	Duration of oxygen transport. D1, D2 VI [T]
Λ_0	Λ at 0 C. D5 VI
Λ_1	Duration of oxygen transport through tissues. D2 VI [T]
Λ_{10}	Λ_1 at 0 C. D5 VI
λ	Coefficient of the duration of oxygen transport in the vascular system. D2 VI [$T\ W^{-1/3}$]
λ_0	λ at 0 C. D5 VI
μ	Proportionality constant relating natural mortality to metabolic rate. E2 XII [ ]
ξ	The concentration in the cell of certain intermediary metabolic products. D1 [$W\ L^{-3}$]
τ	Temperature in degrees centigrade. [C]
τ_m	The temperature at which an enzymatic process has maximum. C7 XIII [C]
$\tau_{\infty m}$	The temperature at which maximum asymptotic weight is attained. C10 XIII [C]
τ_{mg}	The temperature at which the growth rate is maximal. C12 XIII [C]
ω	Weight of oxygen consumed per unit weight lost during fasting. A10 V [ ]

APP. II. OXYGEN CONSUMPTION AS A FUNCTION OF BODY SIZE THROUGHOUT THE ANIMAL KINGDOM

ESTIMATES OF m AND n

Numerous experiments on oxygen consumption (see Hemmingsen, 1960) have shown that the relationship

$$\frac{dO_2}{dt} = Dw^d \qquad \text{.....(A12)}$$

where D and d are constants is a good approximation over a wide range of body size with d almost independent of the systematical position of the animal when insects are excepted. Few authors, however, state definitely how long the experimental animals had been fasting before the experiments and whether the fasting, if any, had its full effects on the respiration when the oxygen consumption was measured. Equation A12, therefore, is an approximation intermediary between equations A8 and A11 describing the oxygen consumption of fasting and fed fishes, respectively. Hemmingsen estimated $d = 0.75$ as an average for all animal groups. When homoiotherms, insects, and unicellular organisms are excluded, $d = 0.82$ is obtained (data read from Hemmingsen's (1960) fig. 3, 4, 5, 7, and 8). Individual estimates outside the range $2/3 < d < 1$ are rare. Since we have $d \leq n$, estimates of d are underestimates of n.

Winberg (1956, 1961) made a thorough and critical survey of the literature on fish respiration and found, for various systematical and ecological groups of fishes, mean values of d ranging from 0.78 to 0.81. Again, the utilization of the results is restricted by incomplete knowledge of the feeding condition of the animals during the experiment.

APP. III. OXYGEN CONSUMPTION OF A GOLDFISH

ESTIMATES OF k AND ITS TEMPERATURE COEFFICIENTS

Ege and Krogh (1914) owned a particularly sluggish goldfish (*Carassius auratus*) which they used in a series of respiration experiments. The respirational rate was unaffected by narcotics and the fish seemed able to adapt itself rapidly to any temperature between 0 and 28 C. It was usually allowed only 1 or ½ hr for acclimation to another temperature. Yet the results of 24 consecutive experiments were markedly stable and in accordance with Krogh's further work on other animals.

It is not definitely stated that the fish was fasting during the 22 days the experiments lasted, but the care with which many influences were brought under control infers that it probably was. Anyway, we shall assume so.

The interpretation of the experiments is based on equations A8 and C5:

$$-\left(\frac{dO_2}{dt}\right)_{fasting} = \omega\, k\, W^n \qquad \ldots\ldots(A8)$$

$$\frac{1}{k} = {}_k a e^{{}_k p_0 \tau} + {}_k b e^{-{}_k p_2 \tau} \qquad \ldots\ldots(C5).$$

The weight of the fish, W = 9.3 g, is constant. Combining equations A8 and C5 and putting $n = 1$ we have

$$-\left(\frac{dt}{dO_2}\right)_{fasting} = \frac{{}_k a}{\omega W}\, e^{{}_k p_0 \tau} + \frac{{}_k b}{\omega W}\, e^{-{}_k p_2 \tau} \qquad \ldots\ldots(2\text{-}1)$$

which is easily solved if data are available for four equidistant values of τ, particularly when as in the present case the lowest temperature is zero. Let i be the temperature interval and put

$$e^{i\, {}_k p_0} = A,\ e^{-i\, {}_k p_2} = B,$$

$$\frac{{}_k a}{\omega W} = a',\ \frac{{}_k b}{\omega W} = b' \text{ and } \frac{\tau}{i} = T\ (T = 0, 1, 2, 3),$$

then

$$-\left(\frac{dt}{dO_2}\right)_{fasting} = a'\, A^T + b'\, B^T \qquad \ldots\ldots(2\text{-}2).$$

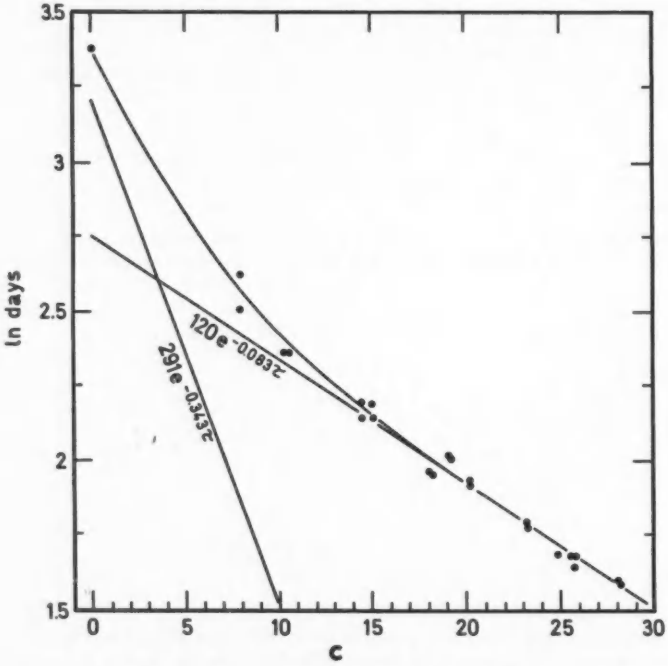
The observations are stated as cm³ of oxygen absorbed per minute and kg of body weight. They can be converted to grams oxygen per day for the whole fish by simple arithmetics, using the approximation $Q_w = Q_v\,(1 - \tau/273)32/22400$, where Q_w is the weight of oxygen in grams and Q_v its volume in cm³. The converted data are plotted against temperature in App. Fig. 1. An eye-fitted curve was read off at the temperatures 0, 8.6, 17.2, and 25.8. C (i.e. $i = 8.6$ C). The four observations were

T $(°C \times 8.6^{-1})$	$-\frac{dt}{dO_2}$ (days g^{-1})
0	41.2
1	74.2
2	29.7
3	14.2

The solution of equation 2-1 by the use of equation 2-2 is

$$-\left(\frac{dt}{dO_2}\right)_{fasting} = 120\ e^{-0.0830\tau} + 291\ e^{-0.343\tau}$$

days per gram oxygen. Because $p_0 < 0$ the two right-hand terms of equation C5 are not distinguishable from each other.



App. Fig. 1. Oxygen consumption of one particular goldfish at a range of temperatures. The curved line is estimated from the model applied. Straight lines represent the two simple exponentials which, on summing, produced the curve. Units on the ordinate are days per gram oxygen absorbed (log scale). App. III.

For $\omega = 0.30$ (see App. IV) and $W = 9.3$ g we further have

$$\left.\begin{matrix} {}_k a \\ {}_k b \end{matrix}\right\} \quad \left\{\begin{matrix} 336 \\ 813 \end{matrix}\right.$$

from which, with equation C5

$$\frac{1}{{}_1 k} = 336\ e^{-0.0830\tau} + 813\ e^{-0.343\tau} \text{ days.}$$

Notice (App. Fig. 1) that the first term alone is a good approximation at temperatures over 12 C. This simplifies the expression to equation C6:

$${}_1 k = k_0\ e^{p_k \tau} \qquad \text{.....(C6)}$$

$${}_1 k = 1.09\ e^{0.0830\tau} \text{ years}^{-1}$$

although the approximation makes the expression more or less empirical because it fits the points at any reasonably short range of temperature, also below 12 C. When its use is not warranted the estimates of k_0 and p_k depend upon the temperature interval covered.

Krogh's goldfish has become famous for the clarity and simplicity of the experiments and particularly because later research on many species and on large materials has confirmed the general applicability of the results (Winberg, 1956).

APP. IV. OXYGEN CONSUMPTION OF FED AND FASTING COD

ESTIMATES OF ωk, p_k, $\omega \alpha h$, m, AND n

A paper by Saunders (1963) contains data for estimation of ωk, $\omega \alpha h$, m, and n from equations A8 and A11.

Saunders (1963) investigated the rate of oxygen consumption in fed and fasting Atlantic cod (*Gadus morhua*) of a size range of 0.1–7 kg. He found that respiration decreased during the 1st week of fasting and, therefore, let the fish fast for 1 week before measuring the fasting metabolism. The experimental device left the fish room for natural behaviour, and no attempt was made to reduce the oxygen consumption to a minimum, as is often done in similar work, e.g. through anaesthetizing the fish or by selecting the lowest respirational rates observed. The oxygne consumption was estimated for fed cod at two temperatures and for fasting cod at three. The results were, in terms of the equation

$$-\frac{dO_2}{dt} = Dw^d \qquad \ldots\ldots(A12).$$

τ (°C)	Fasting: D = ωk (g^{1-n} $years^{-1}$)	Fasting: $d = n$	Fed: D	Fed: d
5	1.59	0.791	–	–
10	1.32	0.886	2.88	0.831
15	1.99	0.845	5.71	0.757
Mean	1.63	0.841		

Oxygen consumption was measured in grams per year and the weight of the fish in grams. For fasting cod D and d are identical with k and n because equation A12 turns into equation A8,

$$-\left(\frac{dO_2}{dt}\right)_{fasting} = \omega\, k\, w^n \qquad \ldots\ldots(A8).$$

The additional parameters, $\omega\, \alpha\, h$ and m, for feeding cod are found by subtracting the oxygen consumption of fasting cod from that of fed ones,

$$\left(\frac{dO_2}{dt}\right)'_{fed} - \left(\frac{dO_2}{dt}\right)_{fasting} = \left(\frac{dO_2}{dt}\right)_{feeding} = -\,\omega\, \alpha\, h\, w^m \quad \ldots\ldots(A10).$$

τ (°C)	$\alpha\, \omega\, h$ (g^{1-m} $years^{-1}$)	m
10	2.05	0.716
15	4.04	0.669
Mean	3.04	0.692

Whereas the estimate of n (= 0.84) is in accordance with the results obtained in other examples, the estimate m = 0.69 is fairly high.

Neither the rate of weight loss during fasting, nor the chemical composition of the cod used were recorded. $\omega = dO_2/dw$, therefore, could not be determined from the material. However, another analysis of the composition of young cod is available (see App. V), namely, $\omega = 0.27$. Hence, $k = 6.0$ $g^{0.16}$ $years^{-1}$ ($\tau = 10$ C) and $\alpha h = 11.3$ $g^{0.31}$ $years^{-1}$ ($\tau = 12.5$ C).

The values of ωk and $\omega \alpha h$ at each temperature can be adjusted to the mean values of m and n by computing the rates of oxygen consumption of fed and fasting cod of about average size (1200 g) by means of the parameter estimates already made. Insertion in equations A8 and A10 with $n = 0.841$ and $m = 0.692$ gives the adjusted estimates:

τ	ωk	$\omega \alpha h$
5	1.12	–
10	1.38	2.51
15	2.04	3.19

The model of the temperature dependence of h and k developed above (equations C4 and C5) are not applicable because four sets of data are required (there are four parameters) whereas only two sets in the case of h and three in the case of k are available. The fact that equation C4 is actually in terms of H is unimportant because according to equations B4 and B8 $H = (1 - \alpha) h$. The frank and almost empirical approximation to equation C5 is applicable, though. We find $\omega k_0 = 3.11$ and $kp = 0.060$.

APP. V. OXYGEN CONSUMPTION AND WEIGHT LOSS IN FASTING TENCH

ESTIMATES OF ω, k, p_k, AND n

Lindstedt (1914) investigated the oxygen consumption of starved tench (*Tinca tinca*), stating for each experiment the temperature, τ, and the weight of the fish, w. Because the same specimens were used several times without being fed, the values of w in successive experiments indicate the weight loss. The weight range of the fish used was 8–240 g, and the temperature range was 0–25 C.

Using approximations, we have from equations A8 and C6

$$-\left(\frac{dO_2}{dt}\right)_{fasting} = \omega\, k_0\, e^{p_k \tau}\, w^n \text{ g days}^{-1}$$

$$-\left(\frac{dw}{dt}\right)_{fasting} = k_0\, e^{p_k \tau}\, w^n \text{ g days}^{-1}.$$

Taking logarithms and applying linear regression analysis with two independent variables (τ and w) gives

$$ln\left(-\frac{dO_2}{dt}\right) = -6.372 + 0.0841\,\tau - 0.7241\, ln\, w$$

$$ln\left(-\frac{dw}{dt}\right) = -5.520 + 0.0962\,\tau + 0.7032\, ln\, w$$

from which

$$ln\left(-\frac{dO_2}{dt}\right) - ln\left(-\frac{dw}{dt}\right) = ln\,\frac{dO_2}{dw} = ln\,\omega = -0.8528 + 0.0121\,\tau - 0.0209\, ln\, w$$

where the two last terms are assumed not to be significant. Thus, $\omega = 0.426$ g oxygen consumed per g weight loss during fasting.

We also have $\overline{n} = 0.714$, ${}_k\overline{p} = 0.090$, and $k_0 = 0.00401\ g^{0.287}\ days^{-1} = 1.46\ g^{0.287}\ years^{-1}$ ω can also be computed from the chemical composition of the fish because according to Krogh (1916) the quantities of oxygen used in catabolic processes are for 1 g of protein: 1.42 g; fat: 2.89 g; carbohydrate: 0.53 g. Analyses of tench are not available, but Åhman and Jørgensen (1964) published analyses of protein and fat contents of whole fish of a number of species. Assuming that there has been a glycogen content of 2% (which does not matter much, anyway) the following estimates of ω could be made:

	ω	
	Range	Mean
Clupea harengus	0.31–0.64	0.46
Clupea sprattus	0.34–0.61	0.47
Osmerus eperlanus		0.32
Mallotus villosus	0.36–0.50	0.43
Rutilus rutilus		0.34

(*Continued*)

	ω		
(Concluded)	Range	Mean	
Belone bellone	0.31–0.45	0.38	
Gadus morhua		0.27	avg 0.30
Merlangius merlangus		0.27	
Trisopterus minutus		0.32	
Micromesistius poutassou	0.23–0.32	0.28	
Boreogadus esmarkii		0.43	
Pollachius virens		0.25	
Perca fluviatilis		0.31	
Trachurus trachurus		0.48	
Ammodytidae sp.		0.39	
Trachinus draco		0.35	
Scomber scombrus	0.35–0.63	0.48	
Zoarces viviparus		0.29	
Eutrigla gurnardus		0.45	
Acanthocottus scorpius		0.31	
Pleuronectes platessa		0.23	
Platichthys flesus			
Microstomus kitt			

The variation is due mainly to differences in fat contents. Species which are usually thin have values of ω about 0.30 (about 2% fat). Similar values are obtained for thin specimens of species (e.g. herring) which sometimes have high fat contents. For such species the methods outlined in the present paper should be used with particular caution because the basic assumption (see Introduction) on constant chemical composition of the fish is not very likely to hold.

The protein contents of the 21 species varies but little. The range is 12.5–17.0% with a mean value of 15.30%. The 95% confidence interval of single observations is 13.19–17.41%.

APP. VI. OXYGEN CONSUMPTION OF SPECKLED TROUT AT DIFFERENT OXYGEN CONCENTRATIONS

ESTIMATES OF Λ, Λ_1, λ, ωk p_Λ, p_{Λ_1}, p_λ, AND p_k

Job (1955) investigated the oxygen consumption of speckled trout (*Salvelinus fontinalis*) of sizes from 5 to 1000 g at oxygen concentrations from 2×10^{-6} to 20×10^{-6} g cm^{-3}. The fish had been fasting for a couple of days. The experiments were made at temperatures of 5, 10, 15, and 20 C, but for the present purpose the results were pooled into two groups, of 5–10 and 15–20 C. "Guesstimates" of the asymptotic rate of oxygen consumption, Q^*, were obtained by putting the highest observed value of the oxygen consumption, Q, (for each body size and temperature) equal to 0.95 Q^*. The data refer to "active metabolism" which means that the fish have been labouring under an unusual stress. The results, therefore, should not be generalized, but considered an example of computation only.

The treatment of the data is essentially fitting them to equation D3:

$$\frac{c}{Q/Q^*} = -(\Lambda_1 + \lambda w^{1/3})\, Q^* + \xi \left(1 - \frac{Q}{Q^*}\right)^{-1} \qquad .....(D3)$$

in order to estimate the transport time (seconds) for oxygen, $\Lambda = \Lambda_1 + \lambda w^{1/3}$ (equation D2). Equation D3 is linear in cQ^*/Q and $(1-\frac{Q}{Q^*})^{-1}$ for any fixed value of body size. For a fish weighing 5 g the data at temperatures of 5–10 C are given in App. Table I where, in units of 10^{-6} g cm^{-3} sec^{-1}, $Q^*\{5\text{ C}\} = -0.0844$ and $Q^*\{10\text{ C}\} = -0.1028$ with the arithmetic mean $Q^*\{7.5\text{ C}\} = -0.0936$. Equation D3 becomes

APP. TABLE I. Oxygen consumption of speckled trout weighing 5 g (App. VI, from Job, 1955).

Temp (C)	Oxygen concn, c 10^{-6}g cm^{-3}	Oxygen consumption, Q 10^{-6}g cm^{-3} sec^{-1}	Relative consumption rate Q/Q^*	$\frac{c}{Q/Q^*}$	$(1-\frac{Q}{Q^*})^{-1}$
5	1.97	−0.0183	0.217	9.08	1.28
5	3.95	−0.0437	0.518	7.63	2.07
5	5.92	−0.0556	0.659	8.98	2.93
5	7.89	−0.0731	0.866	9.11	7.46
5	11.84	−0.0802	0.950	12.46	20.00
10	3.58	−0.0659	0.641	5.59	2.78
10	5.37	−0.0969	0.943	6.69	17.54
10	7.16	−0.0882	0.858	8.34	7.04
10	10.74	−0.0977	0.950	11.31	20.00

$$\frac{c}{Q/Q^*} = 7.4983 + 0.1320\left(1 - \frac{Q}{Q^*}\right)^{-1}$$

with

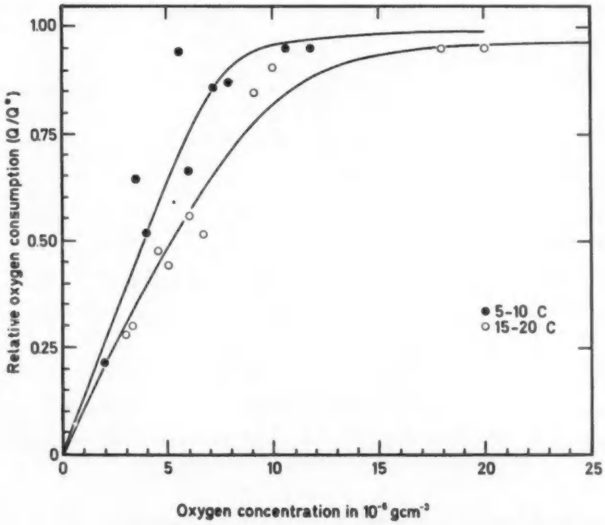
$$-\Lambda Q^* = -(\Lambda_1 + \lambda w^{1/3})\, Q^* = 7.4983 \times 10^{-6}\text{g cm}^{-3}$$

which for $Q^* = -0.0936 \times 10^{-6}$g cm^{-3} gives

$$\Lambda = \Lambda_1 + 1.710\,\lambda = 80.1 \text{ sec.}$$

App. Fig. 2 illustrates the fit of observations to a curve based on the above parameter values, and a similar curve for 17.5 C, again with $w = 5$ g. Separate estimates of Λ_1 and λ require data for other values of w, which were, therefore, estimated in the same way as above:

Weight w, g	Transport time for oxygen (*sec*) $\tau = 7.5$ C	$\tau = 17.5$ C	Ratio $\dfrac{\Lambda\{17.5\text{ C}\}}{\Lambda\{7.5\text{ C}\}}$
5	80	47	0.59
15	100	64	0.64
45	89	86	0.97
135	124	102	0.82
405	139	128	0.92
1000	176	190	1.08



App. Fig. 2. *Salvelinus fontinalis*. Oxygen consumption as a function of oxygen concentration in the water. The curves are estimated from equation D3. App. VI.

The ratios between the two sets of observations indicate the temperature dependence of Λ. The equation

$$\Lambda = \Lambda_0 e^{p_\Lambda \tau} \ (p_\Lambda \text{ negative}) \qquad \text{.....(D5)}$$

gives

$$\frac{\Lambda\{17.5\ \mathrm{C}\}}{\Lambda\{\ 7.5\ \mathrm{C}\}} = e^{10\,p_\Lambda}.$$

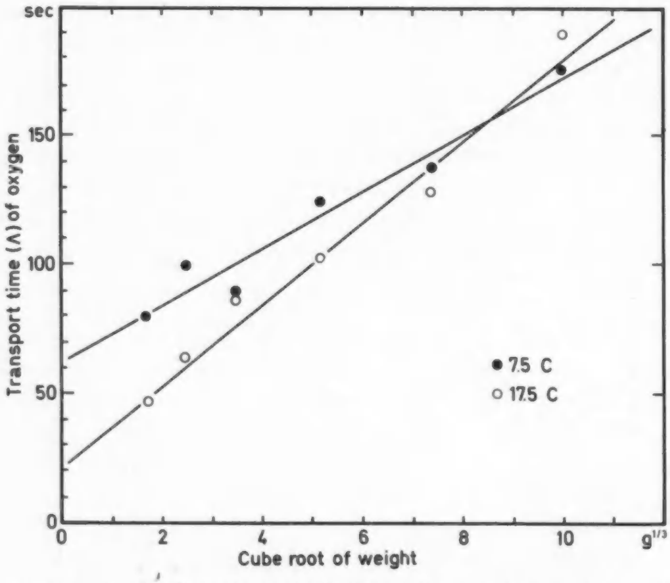
The mean ratio is 0.837 so that $p_\Lambda = -0.018$.

The fit of the above data to

$$\Lambda = \Lambda_1 + \lambda w^{1/3} \qquad \ldots\ldots(\mathrm{D2})$$

is illustrated in App. Fig. 3 where the estimated straight lines have

	7.5 C	17.5 C
Λ_1	62.3	22.2
λ	11.0	16.0.



APP. FIG. 3. *Salvelinus fontinalis*. Estimated duration of oxygen transport in the fish body as a function of body size. App. VI.

The temperature coefficient of Λ_1 is negative, as expected from equation D5:

$$e^{10\,p_{\Lambda 1}} = \frac{22.2}{62.3} = 0.356;\ p_{\Lambda_1} = -0.103$$

whereas that of λ is, surprisingly, positive:

$$e^{10\,p_\lambda} = \frac{16.0}{11.0} = 1.45;\ p_\lambda = 0.037.$$

The reasoning leading to equation D2 may be too simple. It seems possible to argue, e.g. a proportionality with the second power of length, i.e. $\Lambda = \Lambda_1 + \lambda w^{2/3}$. Therefore, the estimates of Λ were fitted also to a second power polynomial,

$$\Lambda = \Lambda_1 + \lambda_1 w^{1/3} + \lambda_2 w^{2/3}$$

with the results:

τ	7.5 C	17.5 C
Λ_1	69.5	33.7
λ_1	7.70	10.6
λ_2	0.288	0.466
$s^2\left\{\Lambda \mid w^{1/3}\right\}$	80.6	72.5
$s^2\left\{\Lambda \mid w^{2/3}\right\}$	103	111
$s^2\left\{\Lambda \mid w^{1/3}, w^{2/3}\right\}$	100	77.3

The smallest variance is obtained by means of equation D2 which therefore cannot be rejected for the present.

An estimate of ωk and of the temperature coefficient, p_k of k (equation C6) can be based on Job's (1955) Fig. 2 which gives the rate of oxygen consumption for $w = 1$ g as:

	Oxygen consumption	
Temperature τ, C	Active metabolism ωk, 10^{-6} g^{1-n} sec^{-1}	Standard metabolism ωk, 10^{-6} g^{1-n} sec^{-1}
5	0.0752	0.0198
10	0.123	0.0396
15	0.166	0.0554
20	0.305	0.0792

These estimates are independent of n because $1^n = 1$. Fitting linearly (i.e. logarithmically) to equation C6 after multiplication by ω, (equation C4):

$$ln\ \omega k = ln\ \omega k_0 + p_k \tau$$

gives, for active metabolism,

$$ln\ \omega k = -3.0426 + 0.09004\tau$$

$$s^2\ \{\omega k \mid \tau\} = 0.007697.$$

Correcting for the bias introduced with the log transformation (Hald, 1952, p. 161) by adding $s^2/2$ to the logarithmic mean, and taking the antilog leads to

$$\omega k = 0.0479 \times 10^{-6}\, e^{0.0900\,\tau}\, g^{1-n}\, sec^{-1} = 1.51\, e^{0.0900\,\tau}\, g^{1-n}\, years^{-1}$$

for active metabolism and similarly to

$$\omega k = 0.0141 \times 10^{-6}\, e^{0.0899\,\tau}\, g^{1-n}\, sec^{-1} = 0.446\, e^{0.0899\,\tau}\, g^{1-n}\, years^{-1}$$

for standard metabolism. Standard metabolism, it should be mentioned, in Job's (1955) definition is as artificial as active metabolism. It is the lowest metabolic rate observed during a 24-hr experimental period.

Chemical analysis of the fish was not made. In the absence of weight loss data, therefore, ω cannot be estimated. Assuming that trouts are fat we can, however, make a guess by means of the list of calculated ω values given in App. V. $\omega = 0.4$ seems a reasonable value. Thus,

$$k_0 = 3.8 \text{ g}^{1-n} \text{ years}^{-1} \quad \text{for active metabolism}$$

$$k_0 = 1.1 \text{ g}^{1-n} \text{ years}^{-1} \quad \text{for standard metabolism}$$

The value for normal behaviour should be found between these extremes.

APP. VII. GROWTH AND FEEDING OF PLAICE

Estimation of Metabolic Parameters of Young Plaice

ESTIMATES OF m, k, h_1, h_2, H, f, α, AND W_∞

Dawes (1930, 1931) fed young plaice (*Pleuronectes platessa*) varying quantities of mussel meat and found the growth rate. The material is to some extent unsatisfactory; yet it provides data for estimation of several parameters introduced in the paragraph on Growth and Food. For simplicity it shall be assumed that mussel meat is identical with plaice meat. A correction for differences of available free energy per gram would enter the expression for the ration which would have to be multiplied by a conversion factor in order to change the ration actually eaten to the equivalent amount of fish.

Estimates of n, the parameter of the dependence of fasting catabolism upon body size, cannot be made. Results obtained in several other examples indicate that $n = 5/6$ is a fairly good guess, and it shall be used.

m, the corresponding parameter of anabolism, can be estimated by plotting ration against weight on a log scale (equation B2):

$$\frac{d\mathrm{R}}{dt} = h_1 f w^m,$$

using data for any given feeding level (i.e., f constant, $f \neq 0$). Bückmann (1952, p. 12) compiled data from Dawes's experiments and from his own, using plaice given surplus food. The results are widely varying:

	m
Dawes	0.65
Bückmann 1950 expt.	0.53
" 1951 expt.	0.34

ranging, in fact, from 1/3 to 2/3. For the present purpose, the estimate from Dawes's experiments shall be used, only rounded off for convenience to 2/3. The corresponding solution for the coefficient of anabolism is $h_1 f = 0.299$ g$^{1/3}$ days^{-1}.

The material is not ideal for estimating the coefficient of fasting catabolism, k, but there are two ways of doing it. One fish (A1, Table I, Dawes, 1930, p. 148) lost weight steadily during 4 months and eventually died. Odds are that for some reason, this fish did not eat at all. Fitting the weight-at-time data to equations A14 and A15 as if a deliberate fasting experiment had been made gives, with $n = 5/6$, $k = 0.00734$ g$^{1/6}$ days^{-1}. For fish given surplus food, growth data can be compiled for 18 incidents of plaice weighing about 36 g and for 15 incidents of plaice weighing about 51 g. Here, as elsewhere in the present example, observations at extreme temperatures were omitted, so that the experiments can be considered made at about 16 C. We find

w (g)	36	51
dw/dt (g days^{-1})	0.30	0.37

which, inserted in $dw/dt = \mathrm{H}w^{2/3} - kw^{5/6}$, gives

$$\mathrm{H} = 0.04091 \text{ g}^{1/3} \text{ days}^{-1}$$
$$k = 0.00737 \text{ g}^{1/6} \text{ days}^{-1}.$$

Since the two estimates of k coincide, we can put $k = 0.0074$.

Equations B3 and B8 give

$$\frac{dw}{dt} + k\,w^n = (1-\alpha)\,h_1\,f\,(1-e^{-h_2 f^{-1}})\,w^m \qquad \ldots\ldots(6\text{-}1)$$

the left side of which is determined by sets of observations of growth rate and weight when k and n are already known. The right-hand term contains the ration eaten, $d\mathrm{R}/dt$, factored into

$h_1 f w^m$ where m is known. f, however, is unknown, as are also α and h_2. Putting $f = 1$ for Dawes's "maximum feeding" is scarcely warranted because Bückmann (1952) found that the ration eaten depends upon the amount of surplus food given:

Given, g	Eaten, g
546	264
273	206
182	166
137	134

An ogive with higher and lower asymptotes is indicated, but Dawes's data do not allow an estimate of f. Models by Ivlev (1961) and Rashevsky (1959) are perhaps applicable but there are problems, inconvenient to tackle in the present context. Remembering that the present computation is to be considered an example only, we shall put $f = 0.9$ for "maximum feeding." For estimation of parameters of equation 6-1 two sets of data are necessary. Let one be the already used fish weighing about 51 g and fed surplus food ("maximum requirements") and let the other be the mean values for 11 incidents when fish weighing about 31 g were fed maintenance ration, or approximately so. We have

	"Maintenance"	"Maximum"
w (g)	31	51
$\frac{dw}{dt}$ (g days^{-1})	−0.01	0.37
$\frac{dR}{dt}$ (g days^{-1})	0.54	3.69

Thus, for "maximum" ($f = 0.9$):

$$h_1 = \frac{dR/dt}{f\ w^m} = \frac{3.69}{0.9 \times 13.8} = 0.297 \qquad \ldots\ldots(6\text{-}2)$$

and, by means of h_1, for "maintenance":

$$f = \frac{dR/dt}{h_1\ w^m} = \frac{0.54}{0.29 \times 9.87} = 0.184.$$

Inserting $h_1 = 0.297$ into $h_1 f = 0.299$ which was found above, gives $f = 1$ for "maximum feeding." Putting $f = 1$ in equation 6-2, however, does not make the agreement any better. The difference is ascribed to the variance of the mean values used.

Note, that the value of f for maintenance refers to $w = 31$ g specifically. For increasing weight the maintenance f increases towards 1. It is also important that feeding maintenance ration to a fish of weight w amounts to putting $w = W_\infty = \varphi(f)$.

Inserting the two sets of data tabulated above, with the respective values of f, in equation 6-1 gives solutions, first for h_2 by iteration, and then for α:

$$h_2 = 1.026;\ 1-\alpha = 0.223;\ \alpha = 0.777.$$

$(1-\alpha)$ is, to a first approximation, the efficiency of energy transfer (and α, the entropy increase).

The constant parameters now known, the dependence of some quantities upon f can be tabulated, namely the instantaneous coefficient of net anabolism,

$$\mathrm{H} = (1-\alpha)\, h_1 f\, (1-e^{-h_2} f) \qquad \ldots\ldots(\mathrm{B9})$$

the asymptotic weight,

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad \text{.....(A19)}$$

and the maintenance ration,

$$(dR/dt)_{maint} = h_1 f_{maint} W_\infty{}^m \qquad \text{.....(B14).}$$

f	H ($g^{1/3}$ $days^{-1}$ × 10^2)	$w = W_\infty$ (g)	$(dR/dt)_{maint}$ (g $days^{-1}$)
0.10	0.663	5.60×10^{-1}	2.02×10^{-2}
0.15	0.993	6.34	1.53×10^{-1}
0.184	1.22	2.12×10	4.19×10^{-1}
0.20	1.32	3.47×10	6.30×10^{-1}
0.25	1.63	1.24×10^2	1.84
0.40	2.45	1.42×10^3	1.50×10
0.47	2.76	2.95×10^3	2.87×10
0.60	3.26	7.81×10^3	7.06×10
0.80	3.83	2.10×10^4	1.81×10^2
0.90	4.06	2.95×10^4	2.55×10^2
1.00	4.25	3.90×10^4	3.42×10^2

The estimate of H for $f = 0.9$ is in agreement with the one obtained above, $H = 4.09 \times 10^{-2}$, when estimating k. The asymptotic weight of North Sea plaice, $W_\infty = 2.9 \times 10^3$ g, as estimated by Beverton and Holt (1957) corresponds to $f \approx 0.47$ which means that North Sea plaice eat half as much as those of Dawes's plaice given mussel meat in surplus. The result seems plausible. The underestimate of the maintenance ration for $f = 0.184$, where 0.42 g was expected and 0.54 g observed, is probably due to inaccuracies of the estimates of k and f.

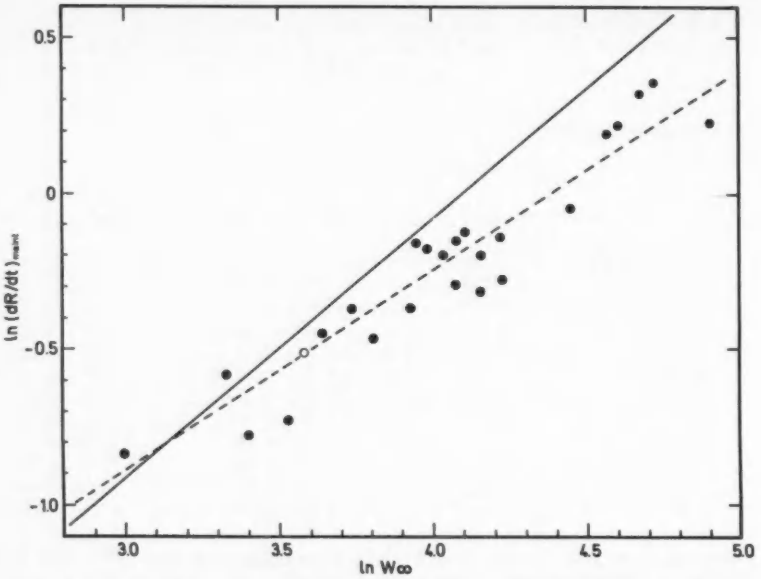
App. Fig. 4 is a plot of $ln\ (dR/dt)_{maint}$ against $ln\ w = ln\ W_\infty$. Individual entries are 26 maintenance experiments by Dawes. The period of observation was over 100 days, the temperature between 13 and 19 C, and the total change in weight less than ±0.5 g. The broken line shows the best fit of these points to a straight line. The slope is 0.63 with 95% confidence intervals of 0.42–0.84. The solid line shows the maintenance ration according to the present model, as computed above. It has a slope of $0.83 = n$ within the range of w considered. For higher values of w the slope increases slowly as required in the model according to which it is $\geq n$ (equation B13 and the text connected with it). Beverton and Holt (1957) accepted the slope estimated from Dawes's data at its face value, putting for simplicity $(dR/dt)_{maint} = C\ w^{2/3}$ and incorporated this expression in a model of growth and feeding. Paloheimo and Dickie (1966a), however, computed the metabolic rates of Dawes's plaice, plotted them against weight, and found suspiciously shallow slopes for the fish fed maintenance rations as well as for those fed in surplus. Thus, Dawes's data may be biased in some way.

The feeding level, f_{max}, ensuring maximum utilization of food is a function of body size and is determined by

$$f_{max} = -\frac{h_2}{ln\ \dfrac{k}{h_1\ h_2\ (1-\alpha)} + (n-m)\ ln\ w} \qquad \text{.....(B22)}$$

whereas the maximum instantaneous efficiency of utilization of total food for growth is given by equations B21 and B22 as

$$u_{max} = (1-\alpha)\ (1-e^{-h_2/f_{max}}) - \frac{k\ w^{n-m}}{h_1\ f_{max}} \qquad \text{.....(6-3)}$$



APP. FIG. 4. Maintenance ration of plaice plotted against weight, both on a log scale. Data from Dawes. The broken line is a least square fit to individual observations. The full line is that expected from the model. The difference is not significant at the 95% level. App. VII.

and the ration to ensure maximum utilization is (from equation B2)

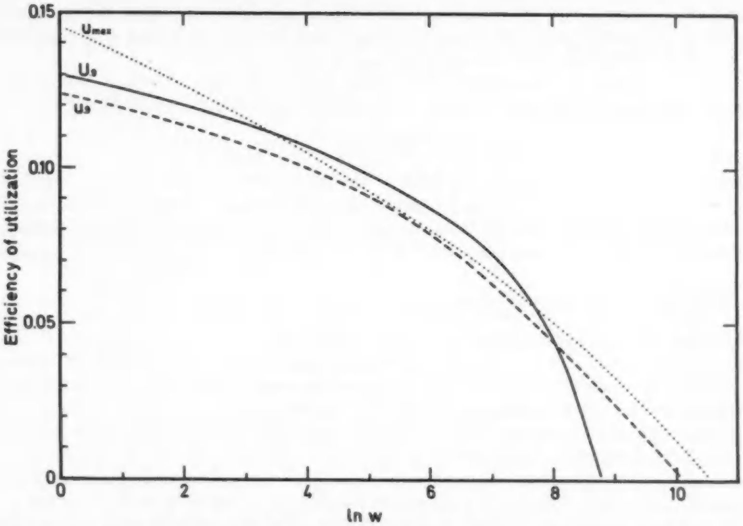
$$\left(\frac{dR}{dt}\right)_{max} = h_1 \, f_{max} \, w^m \qquad \ldots\ldots(6\text{-}4).$$

These quantities are tabulated below. The lowest weight for which full ration is the most efficient is found by putting $f_{max} = 1$ in equation B22 and solving for w. $u_{max} = 0$ is the limiting case for which full ration is maintenance ration (bottom row of the foregoing table). It leads to $W_{\infty max}$ (here 39 kg) and is independent of the rations given to the younger stages (the mysterious "equifinality of growth" of early authors).

We have:

w (g)	f_{max}	u_{max}	$(dR/dt)_{max}$ (g days^{-1})
10^{-2}	0.342	0.179	4.71×10^{-3}
10^{-1}	0.392	0.164	2.50×10^{-3}
1	0.460	0.146	1.37×10^{-1}
10	0.555	0.123	7.66×10^{-1}
10^{2}	0.701	0.0960	4.48
10^{3}	0.951	0.0654	2.83×10
1.39×10^{3}	1.000	0.0610	3.68×10
10^{4}	1.000	0.0291	1.38×10^{2}
3.90×10^{4}	1.000	0.0000	3.42×10^{2}

u_{max} is plotted against weight in App. Fig. 5.



APP. FIG. 5. Estimates of food utilization for growth by plaice based on Dawes' data and plotted against weight on a log scale. u_{max}: maximum efficiency ($f = f_{max}$); $u_{.9}$: efficiency at constant feeding level, $f = 0.9$; $U_{.9}$: efficiency of total food consumed during the life of the fish. In principle an integration of $u_{.9}$, but using different approximations. See also tables in the text and App. VII.

For constant f the total amount of food consumed by any one fish of weight w_t up to time t is given by

$$R_t = \frac{h_1 f W_\infty^{2/3}}{2K}\left(2Kt + (1-e^{-2Kt}) - 4(1-e^{-Kt})\right) \qquad \ldots\ldots (B25)$$

where W_∞ and $K = k/3$ are estimated from equation 1, i.e. with $m = 2/3$ and $n = 1$. The growth rate data used above to determine k and H for $m = 2/3$ and $n = 5/6$ give, for $m = 2/3$ and $n = 1$:

$$K = 0.0006027 \text{ days}^{-1}$$

$$W_\infty = 6352 \text{ g}.$$

These, inserted in equation B25 with $f = 0.9$ and in equation A28 with $t_0 = 0$, give total food consumed, weight-at-time, and, by division, the efficiency U of utilization of total food for growth (equation B26):

t (days)	R_t (g)	w_t (g)	U	u
100	8.35	1.28	0.130	0.122
200	8.12×10	9.36	0.115	0.111
400	5.98×10^2	6.28×10	0.105	0.098
800	4.04×10^3	3.57×10^2	0.0885	0.080
1600	2.35×10^4	1.51×10^3	0.0642	0.066
3200	1.08×10^5	3.97×10^3	0.0368	0.057
∞	∞	6.35×10^3	0	0.029

The last column shows the instantaneous efficiency, u, computed as before but with $f = 0.9$ throughout. Full agreement between the curves for U and u cannot be obtained because different approximations to the growth function were used (App. Fig. 5).

When maintenance requirements are covered additional food consumed will be utilized for growth independently of body size and with an efficiency given by equation B20, e.g.:

$$v = (1-\alpha)\,(1-e^{-h_2/f}) = 0.152 \quad \text{for} \quad f = 0.9.$$

When considering the results obtained in the present example it should be remembered that there is reason (Bückmann 1952) to believe that the plaice in Dawes's experiments shared the rations with crustaceans entering the well boxes in which the fish were kept. Accordingly, all coefficients of utilization are suspected to be underestimates.

Some Population Parameters for North Sea Plaice

ESTIMATES OF ${}_{pop}R$, ${}_{pop}R_{mr}$, ${}_{pop}R_g$, A.P., AND ${}_{pop}U$

The above results can be utilized on the population level if some additional parameters are available as for instance for North Sea plaice, so thoroughly analyzed by Beverton and Holt (1957). Unfortunately these authors were dealing almost exclusively with the stock of adult plaice so that in order to make the computations as an exercise we must assume that the growth and metabolic parameters in young plaice are the same as in adults. We shall compute the whole food consumption of the adult population and partition the consumption into maintenance requirements and growth food (${}_{pop}R$, ${}_{pop}R_{mr}$ and ${}_{pop}R_g$, equations B28–B30). Also the annual production (A.P., equations B31 and B32) and the efficiency of utilization of total food for growth by the population (${}_{pop}U$, equation B33) shall be computed.

Since the feeding level of North Sea plaice is not known a priori, it is necessary to take the observed growth curve as an exit. The Pütter parameters (equation A28) as estimated by Beverton and Holt are: $W_\infty = 2867$ g, $K = 0.10$ years^{-1} and $t_0 = -0.82$ years. From these authors we shall also take the age at recruitment, t_r, the total mortality coefficient, Z, and the annual number of recruits, N_r (R in the terminology of Beverton and Holt):

$$t_r = 3.72 \text{ years}, \; Z = 0.83 \text{ years}^{-1}, \; N_r = 2.8 \times 10^8.$$

Accepting t_0 as the birthday of the plaice we can put

$$_0t_r = t_r + t_0 = 4.54 \text{ years}$$

and

$$N_r = N_0\, e^{-4.54Z} = 2.8 \times 10^8; \; N_0 = 2.8 \times 10^8 \times e^{3.77} = 1.2 \times 10^{10}$$

where N_0 is fictitious because the pre-recruit mortality is not known. The feeding level, f, was estimated above by means of the W_∞ of Beverton and Holt, and for n a value of 5/6 again has to be assumed. The other parameters are estimated from Dawes's data. Thus,

$$f = 0.47; \; n = 5/6; \; m = 2/3; \; h_1 = 0.297 \text{ g}^{1/3} \text{ days}^{-1}$$

$$h_2 = 1.03; \; \alpha = 0.777; \; k = 0.0074 \text{ g}^{1/6} \text{ days}^{-1}.$$

These estimates were made at a temperature of approximately 16 C, which affects the values of h_1 and k. A reduction to 10 C, the approximate mean temperature of the North Sea, has to be made. In a previous paper (Ursin, 1963a, Fig. 4) was estimated the variation with temperature of a quantity (the growth rate of very young plaice) almost proportional with h_1. The correction factor from 16 to 10 C is 0.79. The temperature correction for k can be based on results obtained for goldfish in App. III, because there is evidence (Winberg, 1956) that the temperature relations of catabolic processes do not differ appreciably from one species to another. The estimates based on a fit of data to equation C5 (the elaborate one with four parameters) show that the correction factor is 0.71. Therefore, changing also the time unit, we have

$$\tau = 10 \text{ C}: \; h_1 = 0.297 \times 0.79 \times 365 = 85.6 \text{ g}^{1/3} \text{ years}^{-1}$$

$$k = 0.0074 \times 0.71 \times 365 = 1.92 \text{ g}^{1/6} \text{ years}^{-1}$$

further

$$\beta = 1-e^{-h_2/f} = 0.888;\ v = (1-\alpha)\ \beta = 0.198;\ H = v\ h_1 f = 7.97.$$

The next step is to evaluate the integral

$$J_x = \int_0^t (1-e^{-Kt})^{3x} \ e^{-Zt}\ dt \qquad \ldots\ldots(50)$$

for $x = m = 2/3$ and for $x = n = 5/6$, and both for $t = \infty$ and $t = {}_0t_r$.

The method is indicated in equation B34: evaluating J_x for $x = \{0, 1/3, 2/3, 3/3, 4/3\}$ and interpolating graphically. The results were

	$t = \infty$	$t = 4.54$	Difference
J_0	1.20482	1.17610	0.02782
$J_{1/3}$	0.12955	0.11750	0.01205
$J_{2/3}$	0.025155	0.019829	0.005326
$J_{3/3}$	0.006678	0.004271	0.002407
$J_{4/3}$	0.002171	0.001056	0.001115
$J_I = J_{2/3}$			0.00533
$J_{II} = J_{5/6}$			0.00358

Of course, the choice of $m = 2/3$ saves one interpolation.

We can now compute, for the adult population (from $t = {}_0t_r$ to $t = \infty$)

$$_{pop}R = h_1 f\, W_\infty^{\ m}\, N_0 \int_{{}_0t_r}^{\infty} (1-e^{-Kt})^{3m}\ e^{-Zt}\ dt \qquad \ldots\ldots(B28)$$

$$= 85.6 \times 0.47 \times 2867^{2/3} \times 1.2 \times 10^{10} \times 0.00533 = 5.2 \times 10^{11} g$$

which is the food eaten by one year-class from recruitment to death, or by all year-classes in 1 year. Assuming that the North-Sea population of adult plaice is distributed over 10^{11} m^2 puts the annual consumption to 5.2 g of mussel meat per m^2, or probably 10 g of bottom animals, shells etc. included.

For most purposes it is perhaps more convenient to compute food consumption etc. per recruit, using $N_r = N_0\, e^{-(t_r-t_0)Z} = 0.0231\, N_0$. Thus,

$$_{pop}R/N_r = 1877 \text{ g}$$

and similarly, by means of equations B29 – B33:

$$_{pop}R_{mr}/N_r = 1145 \text{ g};\ _{pop}R_g/N_r = 732 \text{ g}$$

$$A.P./N_r = \begin{cases} 145 \text{ g} \quad (B31); \\ 103 \text{ g} \quad (B32); \end{cases} \qquad _{pop}U = \begin{cases} 0.077 \ (B33 \text{ and } B31) \\ 0.055 \ (B33 \text{ and } B32). \end{cases}$$

On contemplating the overall efficiency of food utilization, which is very low, 5–8%, two things should be considered. The figure is too low if, as mentioned above, some of the food of Dawes's plaice was actually eaten by amphipods. Moreover, $_{pop}U$ is not a measure of the efficiency of energy transfer because a fraction, $1-\beta$, of the ration is not utilized by the fish at all. There are also losses through urine which are not specified in the model (included in α).

APP. VIII. WEIGHT LOSS OF FASTING *LEBISTES* MALES

ESTIMATES OF k AND p_k

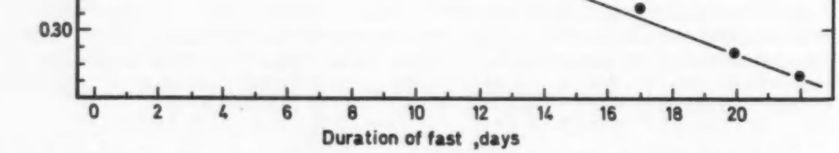
Over 100 male guppies (*Lebistes reticulatus*) were reared in the laboratory by Mr Chr. Frandsen at constant temperatures between 16.5 and 32.0 C. They were progeny of fish obtained from the Botanical Gardens of Copenhagen, where a population had been kept for many years without introduction of fish from elsewhere. When 1–1½ years old, they were starved for about 3 weeks while being weighed with a few days' interval. During fasting they were kept in half-litre jars lowered into the 6-litre jars in which they had been reared and where the females of the same batch were still present. The temperatures were those at which the fish had been reared. The water in the small jars was renewed, and the jars cleaned, every day. There was no aeration and no heating apparatus in the small jars. The chance that the fasting fish should find anything to eat was small. There were 1–11 fish in each jar, 4 on an average. The mortality during the fast was generally small, until the fish had lost about 20% of the initial weight which seems to be what a male guppy can stand loosing without suffering permanent injury. Fish reared below 18 C could not fast successfully; most of them died after a few days, having suffered a weight loss as high as those starved at 30 C. These fish were omitted from the computations.

k was estimated for each fish from

$$ln\ w_t = ln\ w_0 - {}_1kt \qquad \text{.....(A14)}$$

this being made possible by individual differences of colour pattern and fin shape. There was no obvious deviation from the expected straight-line relationship except that sometimes, towards the end of an experiment, the weight suddenly increased, probably as a result of disturbance of the water balance in the body. In such cases, the last observations were discarded. In App. Fig. 6 and the table below are given the average weights of the largest batch (11 fish) during 22 days of fasting at 22.2 C; all specimens survived.

Days t	Mean weight w (g)	*ln* mean weight $ln\ w + 2.3026$
0	0.1424	0.4400
2	0.1382	0.4098
6	0.1353	0.3883
9	0.1319	0.3635
14	0.1278	0.3316
17	0.1254	0.3128
20	0.1221	0.2861
22	0.1205	0.2730



APP. FIG. 6. *Lebistes*: 11 males. Mean weight (log scale) during fasting at 22.2 C. App. VIII.

The total loss was 15% of the initial weight. Equation A14 gives ${}_1k = 0.007222$ days^{-1} $= 2.638$ years^{-1}. Using equation A14 means putting $n = 1$. The correction for $n \neq 1$ is given by equation A15 as $(1-n)\ ln\ w_0$. For $n = 5/6$ the corrected value is ${}_{5/6}k = 1.93$ g$^{1/6}$ years^{-1}. Since the weight of *Lebistes* males deviates from unity (gram) by one size order only, the difference between ${}_1k$ and ${}_nk$ $(n \neq 1)$ is smaller than in most other fishes. As the material does not permit an estimate of n, the approximation $n = 1$ has been used throughout.

App. Table II and App. Fig. 7 show $ln\ k$ as a function of temperature. The fitted regression line (equation 14) is

$$ln\ {}_1k = 0.04914 + 0.4765\ \tau$$

$$s^2 = 0.05433 \text{ (average)}$$

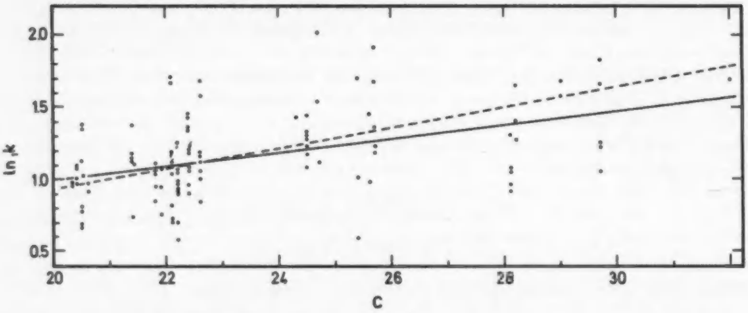
correction for ln transformation $= s^2/2 = 0.02716$, approximately

corrected equation: $$ln\ {}_1k = 0.07630 + 0.04765\ \tau$$

$${}_1k_0 = 1.08 \text{ years}^{-1},\ p_k = 0.0476.$$

App. Table II. Rate of weight loss expressed as $ln\ k$ (where $\frac{-dw}{dt} = k\ w$) in 110 *Lebistes* males kept fasting at the temperatures at which they had been reared. Each row indicates an individual experiment. (See App. Fig. 6, App. VIII.)

Temp (C)	ln k										
32.0	1.69										
29.7	1.05	1.22	1.24	1.66	1.85						
29.0	1.58	1.68									
28.2	1.27	1.41	1.65								
28.1	0.91	1.06	1.06	1.07	1.30						
25.7	1.17	1.23	1.37	1.67	1.90						
25.6	0.98	1.45									
25.4	0.58	1.01	1.69								
24.7	1.12	1.54	2.01								
24.5	1.30										
24.5	1.07	1.17	1.22	1.23	1.29	1.31	1.44				
24.3	1.43										
22.6	0.84	1.12	1.17	1.58	1.68						
22.6	1.00	1.05	1.17								
22.4	1.07	1.18	1.18	1.24	1.34	1.34	1.42	1.45			
22.4	0.90	0.96	1.07	1.20	1.26	1.45					
22.2	0.58	0.70	0.91	0.91	0.93	0.97	0.98	1.04	1.07	1.21	1.25
22.1	0.73	1.14	1.16								
22.1	0.71	0.82	1.04	1.11	1.16	1.71					
22.1	1.66										
21.9	0.75	0.95	1.08								
21.8	0.85	0.95	1.03	1.10							
21.4	1.11	1.12	1.15	1.37							
21.4	0.73	1.18									
20.6	0.91	0.97									
20.5	0.68	1.12	1.38								
20.5	0.67	0.77	0.80	1.02	1.35						
20.4	0.97	1.00	1.09	1.09							
20.3	0.97	0.97									



APP. FIG. 7. *Lebistes*. Rate of weight loss, expressed by the coefficient, ${}_1k$, of fasting catabolism (log scale), as a function of temperature. Males fasting at the temperatures at which they were reared. Observations at temperatures of 16.8–17.8 C were discarded together with an aberrant observation at 20.4 C (by $k = 2.38$). The full line is fitted by the method of least squares. The broken line was computed in the same way from 101 observations of males kept at room temperature (about 22 C) until few days before the experiments. See App. Table II. App. VIII.

There is no obvious curvilinear tendency so that the hypothesis of exponential increase (equation C6) cannot be rejected. A rigorous statistical treatment of the material, however, has been refrained from because of irregularities causing the variance about the regression line to vary from one set of data to another. Bartlett's test applied to variances based on four observations at least, gave $\chi^2 = 42.6$ for 18 df $(0.99 < P < 0.995)$.

A similar set of data was procured in the following way. A large number of *Lebistes* males were obtained from the Botanical Gardens of Copenhagen and kept for 1 or several months in a large aquarium in the laboratory. They were transferred, in numbers about 10, to 6-litre jars at temperatures from 16 to 32 C. The temperature change was made at a rate of about 1 C per day. Then the fish were starved for about 3 weeks, the water being changed with a few days' interval. The water was aerated and in some jars were heating or cooling devices. In spite of careful cleaning, some growth of bacteria was noticed in the jars. The fish therefore may have got small amounts of food during the experiment. Again fish kept at 16 C died after a few days.

The result, based on 101 specimens starved at temperatures between 19.5 and 31.7 C was

$$ln\ k = -0.4737 + 0.07095\ \tau$$

$${}_1k_0 = 0.655 \text{ years}^{-1} \text{ (corrected for log transf.)};\ p_k = 0.0710.$$

The line (broken) is entered in App. Fig. 6. It intercepts with the one derived before at room temperature, 22 C, to which the fish had been acclimated before the fasting experiment. There are many possible explanations of the difference between the two lines (which seems to be significant), because many influences were not under control during these primitive experiments. The simplest explanation is, that the difference is due to acclimation. The fish in the first experiment had been acclimated to the experimental temperature for their whole life, in the second for a few days only. Winberg (1956), however, reviewed critically the literature on temperature acclimation in fishes and doubts the reliability of alleged acclimation effects reported by various authors. In the present case many other influences may have interfered.

APP. IX. WEIGHT LOSS OF FASTING FISH OF VARIOUS SPECIES

ESTIMATES OF k AND n

App. Table III lists estimates of the coefficient, k, of fasting catabolism from fasting experiments with various species, from literature and my own observations. As in the preceding examples the estimates were made from

$$ln\ w_t = ln\ w_0 - {}_1kt \qquad \text{.....(A14)}$$

which gives the value, ${}_1k$, which k takes on for $n = 1$. The value ${}_nk$, of k for $n \neq 1$ is given by

$$ln\ {}_nk \approx ln\ {}_1k + (1-n)\ ln\ w_0 \qquad \text{.....(A15).}$$

APP. TABLE III. The coefficient of fasting catabolism, k, determined from the weight loss of fasting fishes, at experimental temperature and adjusted to 20 C by means of the temperature coefficient, $p_k = 0.05$, found in App. IX.

Species	References	Initial weight		Temp (C)	${}_1k_{obs}$ years^{-1}	$ln\ {}_1k_{obs}$	$ln\ {}_1k_{20}$
		w_0, g	$ln\ w_0$				
Anguilla ang.	Reuss and Weinland, 1912, p. 290	0.168	−1.78	18.8	4.64	1.53	1.59
		0.168	−1.78	12.5	3.09	1.13	1.50
	Lipschütz, 1911 p. 123	0.212	−1.55	17.4	6.99	1.94	2.07
	Own observations	0.929	−0.07	20.8	4.94	1.60	1.56
		0.432	−0.84	20.8	6.03	1.80	1.76
		1.19	0.17	19.4	4.74	1.56	1.59
		2.16	0.77	20.1	2.70	0.99	0.99
Tinca tinca	Lindstedt, 1914	140	4.94	13.0	1.18	0.16	0.51
Cyprinus carpio	Ivlev, 1961b, Table 75	0.53	−0.63	22	4.54	1.51	1.41
	Lipschütz, 1911, p.64	1.33	0.29	15.0	2.40	0.88	1.13
	Kestner and Plaut, 1924 (from Knauthe)	601	6.40	18.0	1.31	0.30	0.40
Abramis brama	Ivlev, 1961b, Table 75	0.32	−1.14	22	4.32	1.46	1.36
Rutilus r. caspicus		0.53	−0.63	22	4.66	1.54	1.44
Silurus glanis		0.86	−0.15	22	3.84	1.35	1.25
Lebistes reticulatus	App. VIII	0.13	−2.04	23.6	3.22	1.17	0.99
Carassius auratus	Own observations	2.81	1.03	20	3.11	1.13	1.13
		28.4	3.35	20	1.78	0.58	0.58
Perca fluviatilis		2.46	0.90	18	5.28	1.66	1.76
		6.22	1.83	20.6	5.24	1.66	1.63
		4.31	1.46	21	4.78	1.56	1.51
Gobius sp.		0.500	−0.69	11.5	1.87	0.63	1.06
		0.412	−0.89	15.0	3.58	1.28	1.53
		0.274	−1.29	20.5	5.44	1.69	1.66
Solea solea		2.38	0.87	21.6	3.75	1.32	1.24
Platichthys flesus		4.73	1.55	17.1	3.31	1.22	1.36
		4.98	1.60	17.1	1.99	0.69	0.84
Pleuronectes platessa		4.26	1.45	17.1	1.43	0.35	0.50
	Dawes, 1930 (fish A1)	44.0	3.78	14.8	1.43	0.35	0.61

The fasting experiments were made at different temperatures, most of them not far from room temperature. Adjustment to 20 C was made by means of the temperature coefficient, p_k = 0.05, estimated in App. VIII for male *Lebistes* kept fasting at the temperature at which they had been reared. Thus,

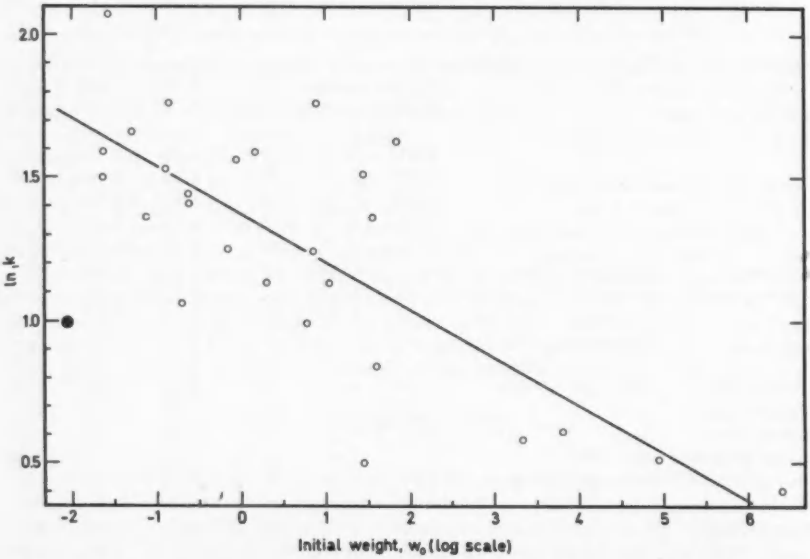
$$k_{20} = k_{obs} \; e^{-0.05\,(T-20)}$$

which holds for any *n*.

Equation A15, rearranged,

$$ln \;\; {}_1k_{20} \approx \overline{ln \;\; {}_nk_{20}} - (1-n) \;\; ln \;\; w_0$$

provides a means of estimating *n* and a mean value of $_nk$ from a straight line if *n* is constant. The notation $\overline{ln \; {}_nk_{20}}$ indicates that the intercept is the mean of the logarithmic values. The independent variable is *ln* w_0. The data in App. Table III are plotted in App. Fig. 8. The value for *Lebistes* males (from App. VIII) is very low. *Lebistes* is, however, the only tropical fish in the assembly and is, therefore, excluded from the computations. Disregarding interspecific differences, the remaining data give



App. Fig. 8. The regression upon body size of the coefficient, $_1k$, of fasting catabolism at 20 C. From weight loss during fasting. Various species, *Lebistes* given special signature. See App. Table III. App. IX.

$$ln \;\; {}_1k_{20} = 1.3753 - 0.1670 \;\; ln \;\; w_0$$

where

$$\overline{ln\ {}_nk_{20}} = 1.3753$$

$$s^2 \left\{ ln\ {}_1k_{20} \mid ln\ w_0 \right\} = 0.08427 \quad (25\ \text{df})$$

$$ln\ \overline{{}_nk_{20}} = \overline{ln\ {}_nk_{20}} + s^2/2 = 1.4175;\ \overline{{}_nk_{20}} = 4.13\ \text{g}^{1-n}\ \text{years}^{-1}$$

$${}_nk_{10} = {}_nk_{20}\, \text{e}^{-10\, p^k} = 2.50\ \text{g}^{1-n}\ \text{years}^{-1}$$

$$s^2\left\{\overline{{}_nk_{20}}\right\} = s^2\left\{ln\ {}_1k_{20} \mid ln\, w_0\right\}\left(\frac{1}{\text{N}} + \frac{(\overline{ln\ w_0})^2}{\text{SSD}\left\{ln\ w_0\right\}}\right) = 0.004357$$

(Hald, 1952, equation (18.4.3)).

95% confidence interval:

$$1.28 < ln\ \overline{{}_nk_{20}} < 1.55;\ 3.6 < \overline{{}_nk_{20}} < 4.7$$

$$1-n = 0.1670;\ n = 0.833 = 5/6$$

$$s^2 \left\{ 1-n \right\} = s^2 \left\{ n \right\} = 0.0007806$$

95% confidence interval of n: 0.78–0.89

Ivlev (1961b, Table 79) investigated the weight loss at complete fasting of 12 species of fish living in the southern part of the Soviet Union. The initial weight was not stated, but all the fish were 25–30 days old at the beginning of the fast. Thus, they must have been of approximately the same size and the k values, therefore, directly comparable. What makes these experiments particularly interesting is the wide range of asymptotic size of the species in question. There are among them three small species and two very big ones. Any dependence of k upon asymptotic size (i.e. "the size of the species") as opposed to the actual size of the experimental animal should come out clearly in these circumstances. The asymptotic sizes of the experimental animals are not known, of course, but I haye (App. Table IV) entered a tentative value for each species. It is quite obvious that k and W_∞ are not correlated to any appreciable extent.

APP. TABLE IV. The coefficient of fasting catabolism, k, at 20 C determined from the weight loss during fasting. All fish were 25–30 days old. W is a very rough guess of the asymptotic size of the species. (App. IX from Ivlev, 1961, Table 79.)

Species	W (g)	${}_1k_{20}$ years^{-1}
Acipenser stellatus	10^5	1.21
Silurus glanis	10^5	1.15
Esox lucius	10^4	1.11
Cyprinus carpio	10^4	1.32
Caspialosa volgensis	10^3	1.01
Tinca tinca	10^3	1.28
Abramis brama	10^3	1.24
Perca fluviatilis	10^3	1.18
Rutilus rutilus caspicus	10^2	1.35
Alburnus alburnus	10	1.36
Neogobius melanostomus	10	1.07
Cobitis taenia	10	1.28

APP. X. GROWTH PARAMETERS ESTIMATED FROM LENGTH-AT-AGE DATA FOR 81 FISH SPECIES

ESTIMATES OF m, n, H, k, W_∞

The present example deals essentially with the application of the generalized growth equation,

$$\frac{dw}{dt} = Hw^m - kw^n \qquad .....(B8)$$

to alleged growth data from field studies. Particularly, it deals with the problem of estimating m and n so that H and k are constant throughout the growth curve. The data were compiled from the easiest available literature. Salmonids were omitted because their growth parameters seemed to fall into two groups, one with very high, another with very small values. Thus, their inclusion would increase unduly the variance. Given the choice of several sets of data for any one species of other families one set was selected which covered a high number of age-groups was based on a large material and was not obviously biased by unsatisfactory methods of sampling. Species and authors are listed in App. Table V.

The first step was to estimate H and k from equation A18, putting $m = 2/3$ and $n = 1$ (Pütter's approximation):

$$\frac{dl}{dt} = \frac{H}{3q^{1/3}} - \frac{k}{3}\,l \qquad ...(9\text{-}1)$$

by fitting annual increments linearly to corresponding body lengths (total lengths; standard and fork lengths were converted). When a weight–length key was given, $q = w/l^3$ was estimated from it. When q could not be estimated a value for a fish of similar shape was inserted. W_∞ was computed from equation A24 as $(H/k)^3$. The estimates are listed in App. Table V.

For further reasoning we shall speak in terms of weight so that

$$\frac{dw}{dt} = Hw^{2/3} - kw \qquad .....(1)$$

is Pütter's approximation to the generalized growth equation

$$\frac{dw}{dt} = Hw^m - kw^n \qquad .....(B8).$$

There are two aspects of the dependence of H and k on body size. These parameters may depend either on the actual size, w, of the animal, or they may depend on the size of the species, i.e. on W_∞. More relevantly, perhaps, the latter possibility could be put: W_∞ may depend on either H or k, or both. Anyway, if H or k, or both, are functions of w because erroneous values of m and n have been used, a false relationship of H and k with W_∞ is introduced when the parameters are estimated from growth curves. Such estimates require a large part of the growth curve and therefore must be based on bigger specimens of a large species than of a small one. In order to avoid this difficulty we shall refer to App. IX where, based on Ivlev's observations, it was found that k is independent of W_∞. When that is so, H must be functionally related to W_∞ because

$$W_\infty = \left(\frac{H}{k}\right)^{\frac{1}{n-m}} \qquad .....(A19)$$

rearranged and in logarithmic form gives

$$ln\,H = ln\,k + (n-m)\,ln\,W_\infty \qquad .....(9\text{-}2)$$

which is linear in ln H and ln W_∞.

APP. TABLE V. Growth parameters estimated from length-at-age data for 81 species of fish (App. X).

			$n=1;\ m=2/3$				$n=0.8321;\ m=0.5611$			m
Reference	Species	$\hat{w}$ 10^2g	$_1k$ y^{-1}	$_1$H cm y^{-1}	$_1W_\infty$ 10^3 g	B	$_nk$ $g^{1-n}y^{-1}$	$_n$H $g^{1-m}y^{-1}$	$_nW_\infty$ 10^3 g	(second estimate)
Hodgson, 1925	*Clupea harengus*	0.41	1.64	8.92	0.164	1.0031	3.49	13.2	0.225	0.55
Motoda, 1963	*Clupea pallasii*	4.3	0.644	5.00	0.469	1.0048	1.79	9.49	0.475	0.62
Iles and Johnson, 1962	*Clupea sprattus*	0.068	1.75	5.47	0.0306	1.0030	2.41	6.70	0.0435	0.57
Phillips, 1948	*Sardinops coerulea*	2.2	0.789	5.01	0.257	1.0047	1.95	8.85	0.263	0.60
Nawratil, 1961	*Sardinops ocellata*	1.1	1.05	7.52	0.369	1.0033	2.32	12.4	0.487	0.60
Bougis, 1952 (after Storrow)	*Sardina pilchardus*	0.93	2.10	9.93	0.108	1.0048	4.48	16.1	0.112	0.42
FAO, 1960 (Nair)	*Sardinella longiceps*	0.41	0.937	5.10	0.160	1.0031	1.73	7.56	0.229	0.63
FAO, 1960 (Ben-Tuvia)	*Sardinella maderensis*	0.49	0.296	2.58	0.672	1.0021	0.57	3.90	1.24	0.74
Bougis, 1952 (after de Navarro)	*Sardinella aurita*	1.2	0.903	6.30	0.337	1.0035	2.01	10.4	0.433	0.61
Bougis, 1952 (after d'Ancona)	*Alosa fallax*	2.7	0.652	7.36	1.47	1.0028	1.66	13.3	2.16	0.65
Frost and Kipling, 1959	*Esox lucius*, males	25	1.26	16.5	2.23	1.0051	4.66	37.6	2.20	0.45
Muir, 1960	*Esox masquinongy*	18	0.210	6.11	24.6	1.0021	0.741	13.5	44.6	0.72
Da Franca, 1953	*Gambusia holbrookii*, females	0.014	2.51	3.34	0.00239	1.0042	2.66	3.47	0.00266	0.65
Hewson, 1955	*Lota lota*	25	0.218	4.78	10.3	1.0031	0.811	10.9	14.5	0.72
Bougis, 1952 (after Letaconnoux)	*Gadiculus thori*	0.18	2.00	6.67	0.0377	1.0039	3.25	9.08	0.0440	0.48
Bougis, 1952 (after Chevey)	*Gadus luscus*	0.93	0.947	5.78	0.221	1.0037	2.03	9.29	0.272	0.59
Kohler, 1964	*Gadus morhua*	16	0.376	9.28	15.2	1.0024	1.30	20.3	25.4	0.67
Ketchen, 1961	*Gadus macrocephalus*	22	1.59	27.2	5.01	1.0038	5.76	61.1	6.11	0.36
Messtorff, 1959	*Merlangius merlangus*, males	1.6	0.813	5.71	0.347	1.0038	1.90	9.74	0.418	0.61
Steele, 1963	*Pollachius virens*	26	0.441	9.11	8.87	1.0033	1.65	20.9	11.8	0.68
Ursin, 1963b	*Boreogadus esmarkii*	0.34	2.13	7.94	0.0509	1.0043	3.86	11.5	0.0563	0.52
Beverton and Holt, 1957 (after Raitt)	*Melanogrammus aeglefinus*	3.0	0.744	7.87	1.19	1.0031	1.94	14.3	1.62	0.61
Bagenal, 1954	*Merluccius merluccius*	16	0.672	17.4	17.7	1.0022	2.32	38.0	30.6	0.62
Orcutt, 1950	*Platichthys stellatus*, females	18	0.823	14.5	5.32	1.0034	2.92	31.9	6.80	0.58
Zemskaja, 1959	*Platishthys flesus*	1.4	1.02	7.15	0.358	1.0037	2.32	12.1	0.444	0.57
Hagerman, 1952	*Microstomus pacificus*, males	2.0	1.47	10.9	0.403	1.0039	3.60	19.1	0.473	0.52

(*Continued*)

App. Table V. Growth parameters estimated from length-at-age data for 81 species of fish (App. X). — (*Concluded*)

			$n = 1$; $m = 2/3$				$n = 0.8321$; $m = 0.5611$			
Reference	Species	$\hat{w}$ 10^2g	$_1k$ y^{-1}	$_1H$ cm y^{-1}	$_1W_\infty$ 10^3 g	B	$_nk$ $g^{1-n}y^{-1}$	$_nH$ $g^{1-m}y^{-1}$	$_nW_\infty$ 10^3 g	m (second estimate)
Rae, 1951	*Microstomus kitt*	2.7	0.822	6.87	0.596	1.0038	2.10	12.5	0.722	0.60
Kändler, 1949	*Rhombus maximus*, females	1.1	0.255	5.06	7.86	1.0012	0.560	8.31	21.0	0.74
Bowers, 1959	*Glyptocephalus cynoglossus*, males	1.8	0.931	7.44	0.513	1.0035	2.23	12.9	0.658	0.60
Kändler and Thurow, 1959	*Limanda limanda*, females	2.2	0.577	6.71	1.56	1.0026	1.43	11.8	2.40	0.67
Tåning, 1948	*Pleuronectes platessa*	3.3	0.663	6.44	1.05	1.0035	1.66	11.8	1.39	0.61
Southward, 1962	*Hippoglossus stenolepis*	72	0.274	8.53	29.4	1.0031	1.22	21.7	41.0	0.69
Sigurdsson, 1956	*Hippoglossus hippoglossus*	123	0.132	8.91	315	1.0017	0.638	24.2	667	0.71
Bagenal, 1955	*Hippoglossoides platessoides*, males	0.27	1.57	5.07	0.0334	1.0046	2.72	7.16	0.0356	0.55
Pruter and Alverson, 1962	*Hippoglossoides robustus*, females	0.34	0.310	2.15	0.337	1.0023	0.560	3.13	0.576	0.74
Beverton and Holt, 1957 (after Bückmann)	*Solea solea*	2.4	1.18	9.75	0.578	1.0037	2.94	17.4	0.710	0.55
Bougis, 1952 (after Furnestin)	*Lepidorhombus whiff-jagonis*	2.0	0.139	4.47	33.2	1.0009	0.304	7.84	161	0.73
Matsuura, 1961	*Pseudorhombus cinnamomeus*	2.8	0.973	8.18	0.596	1.0039	2.51	14.8	0.699	0.55
Miller, 1961	*Gobius paganellus*, females	0.022	1.45	2.64	0.00662	1.0035	1.60	2.87	0.00859	0.50
Bougis, 1952 (after Zei)	*Maena smaris*	0.17	1.50	5.09	0.0389	1.0038	2.44	6.89	0.0463	0.55
Chang, 1951	*Callionymus lyra*, males	0.27	0.789	5.78	0.391	1.0020	1.36	8.15	0.733	0.66
Jones and Hynes, 1950	*Gasterosteus aculeatus*	0.0068	1.50	2.11	0.00277	1.0031	1.42	2.03	0.00377	0.75
Jones and Hynes, 1950	*Pygosteus pungitius*	0.0055	3.65	3.36	0.000787	1.0039	3.29	3.15	0.000854	0.44
Jones, 1953	*Perca fluviatilis*	0.34	0.413	2.53	0.228	1.0026	0.748	3.68	0.356	0.74
Scofield, 1931	*Roccus lineatus*, males	12	0.746	12.8	5.01	1.0031	2.46	27.1	6.97	0.59
Young, 1963	*Paralabrax clathratus*	2.6	0.254	3.94	3.94	1.0020	0.631	7.08	7.49	0.70
Gravier, 1961	*Morone punctata*	6.2	0.225	4.65	8.87	1.0020	0.664	9.19	16.3	0.72
Whitney, 1961a	*Bairdiella isistius*	0.31	2.24	8.13	0.0477	1.0043	3.99	11.7	0.0526	0.41
Joseph, 1962	*Roncador stearnsi*	11	0.838	11.5	2.57	1.0037	2.71	24.0	3.13	0.57

Joseph, 1962	*Menticirrhus undulatus*	6.7	1.10	12.8	1.55	1.0037	3.28	25.3	1.89	0.54
Whitney, 1961b	*Cynoscion xanthulus*	14	2.34	38.9	4.58	1.0033	7.90	83.6	6.02	0.37
Baxter et al., 1960	*Seriola dorsalis*	85	0.385	13.3	41.0	1.0029	1.76	34.5	58.9	0.62
Tsukahara, 1962	*Trichiurus lepturus*	2.9	0.617	8.61	2.71	1.0024	1.60	15.6	4.54	0.67
Bougis, 1952 (after Desbrosses)	*Mullus surmuletus*	1.1	1.48	10.5	0.350	1.0033	3.27	17.2	0.457	0.51
Bougis, 1952	*Mullus barbatus*	0.41	2.18	9.54	0.0839	1.0039	4.07	14.1	0.0990	0.41
Bougis, 1952 (after Heldt)	*Chrysophrys aurata*	6.4	2.00	21.2	1.19	1.0040	5.92	42.0	1.38	0.33
Bougis, 1952 (after Letaconnoux)	*Trachurus trachurus*	0.93	0.574	5.86	1.06	1.0022	1.23	9.46	1.86	0.67
Carlisle et al., 1960	*Amphisticus argenteus*, males	1.4	0.666	6.84	1.09	1.0025	1.53	11.5	1.74	0.64
Bougis, 1952 (after Serbetis)	*Mugil auratus*	2.2	1.01	11.7	1.55	1.0026	2.50	20.6	2.42	0.59
Bougis, 1952 (after Serbetis)	*Mugil capito*	3.6	0.966	12.0	1.94	1.0028	2.60	22.4	2.85	0.58
Bougis, 1952 (after Heldt)	*Mugil cephalus*	10	1.88	25.1	2.39	1.0037	5.99	52.0	2.92	0.34
Clark, 1925	*Leuresthes tenuis*, females	0.27	2.20	7.57	0.0408	1.0043	3.83	10.7	0.0448	0.43
Walford, 1932	*Sphyraena argentea*	8.6	1.09	14.8	2.53	1.0035	3.39	30.3	3.24	0.56
Yunokawa, 1951	*Chelidonichthys kumu*	3.5	0.763	8.96	1.62	1.0030	2.04	16.6	2.31	0.62
Mio, 1961	*Evynnis japonica*	2.5	0.903	11.9	2.26	1.0024	2.28	21.2	3.75	0.59
Pruter, 1954	*Anopoploma fimbria*, males	18	0.705	10.7	3.50	1.0040	2.48	23.6	4.08	0.56
Chatwin, 1958	*Ophiodon elongatus*	50	0.640	13.9	10.3	1.0039	2.67	34.3	12.2	0.56
O'Connell, 1953	*Scorpaenichthys marmoratus*, females	13	1.55	23.5	3.46	1.0036	5.17	50.0	4.33	0.30
Nédélec, 1958	*Scomber scombrus*	3.0	1.20	9.60	0.516	1.0041	3.12	17.5	0.585	0.51
Fitch, 1951	*Pneumatophorus diego*	0.35	0.859	3.26	0.0548	1.0043	1.56	4.75	0.0608	0.63
FAO, 1963 (Yoshida and Otsu)	*Thunnus germo*	57	0.516	15.9	29.4	1.0029	2.20	39.7	43.0	0.61
Tiews, 1957	*Thunnus thynnus*	318	0.402	26.4	284	1.0024	2.29	78.9	467	0.64
FAO, 1963 (Yamanaka)	*Thunnus orientalis*	466	0.523	37.3	364	1.0023	3.18	116	585	0.57
FAO, 1963 (Demir)	*Sarda sarda*	21	0.539	11.4	9.40	1.0027	1.95	25.5	9.45	0.60
FAO, 1963 (Mimura)	*Parathunnus mebachi*	30	0.111	10.5	852	1.0008	0.425	24.5	3125	0.72
FAO, 1963 (Mimura)	*Neothunnus macropterus*	148	0.970	43.6	90.8	1.0027	4.87	120	138	0.48
Shiokawa, 1962	*Sebastes pachycephalus*	0.41	0.552	4.03	0.389	1.0023	1.03	5.96	0.654	0.69
Mio, 1960b	*Sebastes inermis*	0.69	1.10	8.08	0.398	1.0028	2.24	13.6	0.596	0.56
Mio, 1960a	*Sebastiscus marmoratus*	0.41	0.746	6.86	0.778	1.0019	1.39	10.2	1.53	0.65
von Betalanffy, 1951 (after Darjavin)	*Acipenser stellatus*	97	0.162	7.19	87.3	1.0024	0.757	19.0	145	0.72
Bougis, 1952 (after Classen)	*Acipenser sturio*	195	0.288	13.3	98.6	1.0029	1.51	37.7	143	0.66

If the approximations $m = 2/3$ and $n = 1$ made above do not stabilize H and k, the estimates obtained probably correspond to some sort of mean value of the body sizes covered by the material. Let this mean weight be denoted $\hat{w}$. Then, because Pütter's approximation is known to describe satisfactorily the rate of growth of most fishes, we may put

$$\frac{dw}{dt} = {}_1\text{H}\hat{w}^{2/3} - {}_1k\hat{w} = {}_n\text{H}\hat{w}^{m} - {}_n\text{H}\hat{w}^{n} \qquad \ldots\ldots(9\text{-}3)$$

where m and n stand for the values which make H and k independent of w. The suffixes are introduced to avoid confusion of the two sets of parameters. On the further assumption that each term, i.e. each product of a coefficient and a power of weight, is numerically correct, the expressions for H and k in equation 9-3 can be separated:

$$ {}_1\text{H}\hat{w}^{2/3} = {}_n\text{H}\hat{w}^{m};\ ln\ {}_1\text{H} = ln\ {}_n\text{H} - (2/3-m)\ ln\ \hat{w} \qquad \ldots\ldots(9\text{-}4)$$

$$ {}_1k\hat{w} = {}_nk\hat{w}^{n};\ ln\ {}_1k = ln\ {}_nk - (1-n)\ ln\ \hat{w} \qquad \ldots\ldots(9\text{-}5).$$

Notice the similarity of equation 9-5 with equation A15. n and ${}_nk$ are easily determined from equation 9-5 by plotting $ln\ {}_1k$ against $ln\ \hat{w}$ for the individual species listed in App. Table V. Equation 9-4 cannot be utilized in the same way because $ln\ {}_n\text{H}$ is a function of W_∞ (equation 9-2). One problem is the determination of $\hat{w}$ because it is not clear how the mean shall be weighted. The weight of a fish whose length is the arithmetic mean of the mean lengths of individual age-groups has been used: $\hat{w} = q\,\bar{l}^{3}$. App. Fig. 9A is a plot of $ln\ {}_1k$ against $ln\ \hat{w}$ as defined above. Denoting by $\overline{ln\ {}_nk}$ the mean of log values the estimated straight line has the properties:

$$ln\ {}_1k = \overline{ln\ {}_nk} - (1-n)\ ln\ \hat{w} \qquad \ldots\ldots(9\text{-}5)$$

$$ln\ {}_1k = 0.6884 - 0.1679\ ln\ \hat{w}$$

$$s^2\left\{ ln\ {}_1k \mid ln\ \hat{w} \right\} = 0.4256 = s^2\ (79\ \text{df})$$

$$ln\ {}_n\bar{k} = \overline{ln\ {}_nk} + s^2/2 = 0.9012;\ {}_nk = 2.46\ \text{g}^{1-n}\ \text{years}^{-1}$$

$$s^2\left\{ ln\ {}_n\bar{k} \right\} = s^2\left(\frac{1}{\text{N}} + \frac{(\overline{ln\ \hat{w}})^2}{\text{SSD}\left\{ ln\ \hat{w} \right\}}\right) = 0.008349$$

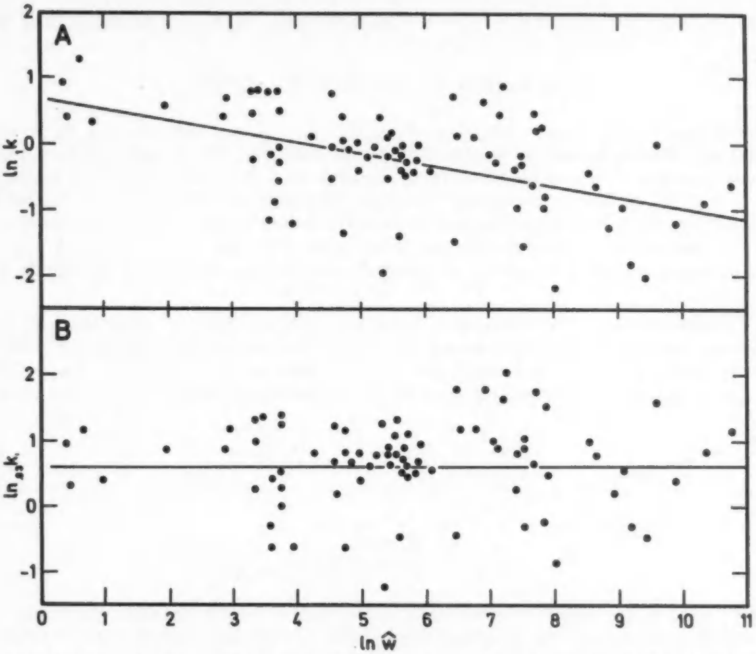
95% confidence interval : $0.72 < ln\ {}_n\bar{k} < 1.08;\ 2.1 < {}_n\bar{k} < 3.0$

$$n = 0.8321$$

$$s^2\left\{ 1-n \right\} = s^2\left\{ n \right\} = 0.0009790$$

95% confidence interval : $0.77 < n < 0.89$.

Most of the species used are from temperate waters, a few are arctic, and some tropical. Therefore, a mean temperature of 10 C seems a good guess. The agreement between the results obtained here and the estimates based on weight loss of fasting animals (App. IX) is striking: $n = 0.83$; ${}_nk_{10} = 2.5$.



APP. FIG. 9. A, the coefficient, k, of fasting catabolism, determined from the catabolic term, $-k\ w$, of the simple growth equation, $dw/dt\ Hw^{2/3} - k\ w$, and plotted against the mean weight, $\hat{w}$, of the fish from which it was determined. B, the same computed from the equation $dw/dt = H\ w^{0.56} - {}_nk\ w^{0.83}$; no significant regression upon body size. From length-at-age data for 81 fish species. App. X.

For the estimation of m an approximation method can be used. Consider equations 9-3, 9-4, and 9-5. An underlying assumption is that the anabolic and catabolic parameters, H and k, of the approximation $dw/dt = Hw^{2/3} - kw$ are correct for one value, $\hat{w}$, of w. This involves that at weight $\hat{w}$ each of the right-hand terms is separately correct. Another assumption is that even the approximation describes a growth curve satisfactorily. Of that there is plenty of evidence in literature. These assumptions have worked well. For body weights different from $\hat{w}$, however, the first assumption (the reliability of each term separately) can scarcely be retained whereas as to the second assumption, there is plenty of evidence in fishery biological literature that it is safe enough. Therefore, we can put

$$\frac{dw}{dt} = {}_1H\hat{w}^{2/3} - {}_1k\hat{w} = {}_nH\hat{w}^{m} - {}_nk\hat{w}^{n} \qquad \ldots\ldots(9\text{-}3)$$

$$\frac{dw}{dt} = {}_1Hw_1{}^{2/3} - {}_1kw_1 = {}_nHw_1{}^{m} - {}_nkw_1{}^{n} \qquad \ldots\ldots(9\text{-}6)$$

where w_1 differs slightly, but distinctly, from $\hat{w}$. Putting $\hat{w} = Cw_1$, C differing enough from one to make rounding off errors from tables inconspicuous, and inserting equations 9-4 and 9-5 gives, after some rearrangement,

$$m = 2/3 - \frac{ln\ B}{ln\ C} \qquad \ldots\ldots(9\text{-}7)$$

where

$$B = \left(1 + \frac{{}_1k}{{}_1H} \hat{w}^{1/3} \left(C^{2/3-n} - C^{-1/3}\right)\right).$$

B was computed for each of the 81 species in App. Table V for $ln\ C = 0.03$, i.e. $\hat{w} = 1.03\ w_1$. The mean and the 95% confidence interval of the mean are 1.00317 ± 0.00062 from which $m = 0.561$ with a 95% confidence interval of 0.540–0.582. This is an underestimate of the real variance because $n = 0.832$ (estimated above) was considered constant instead of being a stochastic variable. As expected, the estimate of m changes slowly with C. Putting $ln\ C = 0.6$ (i.e. $\hat{w} = 1.8\ w_1$) seems to reduce m from 0.56 to 0.54, although the computation was carried through for a few species only.

The estimate $m = 0.56$ was used in subsequent computations. At a late stage of the investigation, however, it was found advisable to check the approximation method by means of the more direct, but also more tedious, procedure of inserting the estimates of ${}_nk_{10} = 2.5$ and $n = 5/6$ from fasting experiments (App. IX) in the growth equation

$$\left(\frac{dl}{dt} + K\,l^{3n-2}\right) = E\ l^{3m-2} \qquad \ldots\ldots(A18)$$

$$K = \frac{k}{3\ q^{1-n}}$$

in order to obtain, by means of a log scale plot, an estimate of $3m$–2 as the slope of a straight line. This was done for each of the 81 species (App. Table V, right-hand column). Interspecific differences of k were neglected, but species-specific values of q were used in the computation of K. The mean of 81 estimates of m was 0.588 (95% confidence limits: ±0.023), which is slightly higher than the figure, 0.561, found by means of the approximation method. The difference was considered too small to warrant an extensive re-computation of subsequent estimates. The new estimates of m had no significant regression upon body size, expressed as $ln\ \hat{w}$. The 95% confidence limits of the slope were 0.12 and –0.0085. Thus the possibility of m varying appreciably with body size or asymptotic size still has to be borne in mind.

Inserting the mean values of m (the first estimate) and n into equations 9-4 and 9-5 for each species provides individual estimates of ${}_nH$ and ${}_nk$ and, by means of equation A19, of ${}_nW_\infty$ (App. Table V). The new values of k are independent of body size. (App. Fig. 9B. The line, $\overline{ln\ {}_nk} = 0.688$ estimated from equation 9-5, is inserted).

The relationship between the estimates of asymptotic weight obtained by means of the two sets of parameters, Pütter's approximation ($m = 2/3$, $n = 1$) and the more correct one ($m = 0.56$, $n = 0.83$) can be expressed by means of equations A19, 9-4, and 9-5 as

$$ln\ {}_nW_\infty = \frac{1}{n-m} \left(\frac{ln\ {}_1W_\infty}{3} - (m + 1/3 - n)\ ln\ \hat{w}\right) \qquad \ldots\ldots(9\text{–}8).$$

With the present estimates, $m = 0.56$ and $n = 0.83$ the foregoing becomes

$$ln\ {}_nW_\infty = 1.23\ ln\ {}_1W_\infty - 0.23\ ln\ \hat{w}.$$

App. Table V gives ${}_nW_\infty = 1.42\ {}_1W_\infty$ as an average for all species.

The variation of ${}_nH$ with ${}_nW_\infty$ is given by equation 9-2 in the form

$$ln\ \overline{{}_nH} = ln\ \overline{{}_nk} + (n-m)\ ln\ {}_nW_\infty$$

which with the above parameter values becomes

$$\ln {}_n\overline{H} = 0.90 + 0.27 \ln {}_nW_\infty .$$

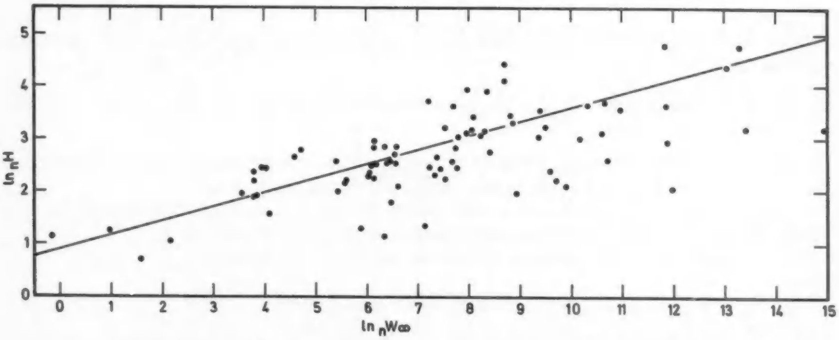
Values of ${}_nH$ for individual species (from App. Table V) are plotted against asymptotic size (log scale) in App. Fig. 10. The line just estimated is inserted. For the approximate size range of fish species,

$$10^{-1}\ \mathrm{g} < W_\infty < 10^5\ \mathrm{g}$$

the range of ${}_nH$ is

$$1.3 < {}_n\overline{H} < 40$$

in terms of $g^{0.44}$ years^{-1}.



App. Fig. 10. The coefficient, H, of net anabolism, computed from the equation $dw/dt = H w^{0.56} - k w^{0.83}$ and plotted against asymptotic weight (log scale) 81 fish species. App. X.

The situation of individual points in App. Fig. 10 reflects that on App. Fig. 9 (k against body size). This is due to the correlation of k with H introduced with the techinque of calculation. Each pair of values was computed from the slope and intercept of one and the same straight line.

APP. XI. SEXUAL DIFFERENCES IN GROWTH PARAMETERS

ESTIMATES OF H, *k*, AND W_∞

The difference between male and female growth curves can be expressed empirically in terms of the growth parameters H (net anabolism), *k* (fasting catabolism) and W_∞ (asymptotic weight). We have from equation A19, arranged as equation 9-2,

$$\ln H_{♀} = \ln k_{♀} + (n-m) \ln W_{\infty ♀} \qquad \ldots\ldots(10\text{-}1)$$

$$\ln H_{♂} = \ln k_{♂} + (n-m) \ln W_{\infty ♂} \qquad \ldots\ldots(10\text{-}2).$$

Assuming a linear relationship between the log scale sexual differences of *k* and W_∞ we have

$$\ln k_{♀} - \ln k_{♂} = A + B\,(\ln W_{\infty ♀} - \ln W_{\infty ♂}) \qquad \ldots\ldots(10\text{-}3).$$

Subtracting equation 10-2 from equation 10-1, solving for $(\ln k_{♀} - \ln k_{♂})$ and inserting in equation (10-3) gives

$$\ln H_{♀} - \ln H_{♂} = A + (n-m+B)\,(\ln W_{\infty ♀} - \ln W_{\infty ♂}) \qquad \ldots\ldots(10\text{-}4).$$

For $A = B = 0$ the differences between male and female parameters are due to differences of H exclusively. For $A = 0$, $B = m-n$, the whole difference is placed upon *k*.

App. Table VI lists male and female parameters for 19 species of fish, one set for each species. The computations were made in the same way as in App. X, putting $n = 0.832$ and $m = 0.561$, as estimated in that example. Fitting to equation 10-3 gives

$$A = -0.02816; \; B = -0.3164$$

$$s^2 \left\{ \underline{\ln k_{♀} - \ln k_{♂}} \;\middle|\; \underline{\ln W_{\infty ♀} - \ln W_{\infty ♂}} \right\} = s^2 = 0.04463$$

$$s^2\{A\} = 0.002839; \quad A/s\{A\} = -0.53.$$

Thus, A is not significantly different from zero and can be neglected. We then have, as the best estimate of a straight line through the origin (Hald 1952),

$$B = -0.3277; \; s^2\{B\} = 0.003677$$

95% confidence interval: $-0.456 < B < -0.200.$

The estimate of $m-n = -0.271$ is within this range. For the present, therefore, the hypothesis $B = m-n$ cannot be rejected and we may put

$$\ln H_{♀} - \ln H_{♂} = 0; \; H_{♀} = H_{♂} \qquad \ldots\ldots(10\text{-}5)$$

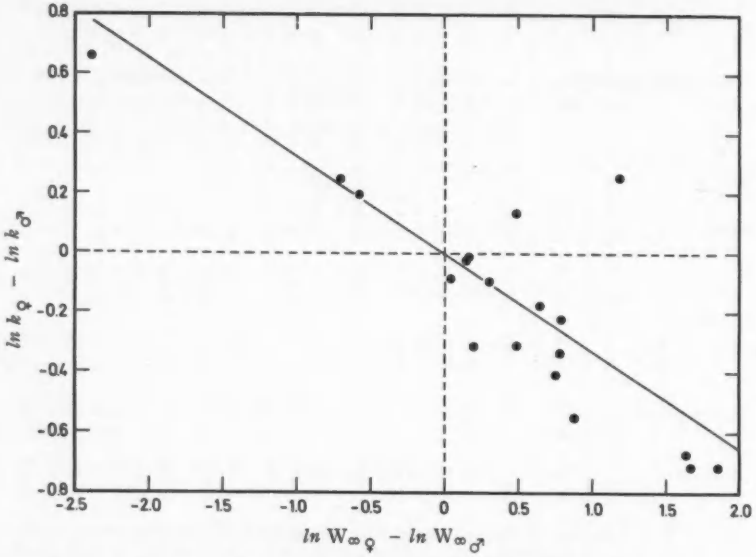
$$\ln k_{♀} - \ln k_{♂} = (n-m)\,(\ln W_{\infty ♀} - \ln W_{\infty ♂})$$

$$W_{\infty ♀} = W_{\infty ♂} \left(\frac{k_{♀}}{k_{♂}} \right)^{\frac{1}{n-m}} \qquad \ldots\ldots(10\text{-}6)$$

for most species, apparently, $k_{♀} < k_{♂}$, as can be seen in App. Fig. 11.

App. Table VI. Growth parameters of males and females of the same species (App XI).

Species	Reference	Males						Females						$ln\,_{n}W_{\infty}$ ♀ − $ln\,_{n}W_{\infty}$ ♂	$ln\,_{n}k$ ♀ − $ln\,_{n}k$ ♂	$ln\,_{n}H$ ♀ − $ln\,_{n}H$ ♂
		$n=1;\ m=2/3$			$n=0.8321;\ m=0.5611$			$n=1;\ m=2/3$			$n=0.8321;\ m=0.5611$					
		$ln\ \hat{w}$	$ln\ _{1}k$	$ln\ _{1}H$	$ln\ _{n}k$	$ln\ _{n}H$	$ln_{n}W_{\infty}$	$ln\ \hat{w}$	$ln\ _{1}k$	$ln\ _{1}H$	$ln\ _{n}k$	$ln\ _{n}H$	$ln_{n}W_{\infty}$			
Mallotus villosus	Pitt, 1958	3.18	1.00	2.40	1.53	2.73	4.43	2.94	1.28	2.48	1.78	2.79	3.72	−0.71	0.25	0.60
Esox lucius	Frost and Kipling, 1959	7.34	0.23	2.80	1.46	3.58	7.80	7.91	−0.42	2.42	0.91	3.26	8.67	0.87	−0.55	−0.32
Gadus morhua	Saemundsson, 1923	7.55	−1.12	2.36	0.15	3.16	11.1	7.62	−1.16	2.37	0.12	3.17	11.2	0.14	−0.03	0.01
Merlangius merlangus	Messtorff, 1959	4.84	−0.207	1.74	0.61	2.25	6.05	4.97	−0.538	1.47	0.30	1.99	6.24	0.19	−0.31	−0.26
Platichthys stellatus	Orcutt, 1950	6.40	0.481	2.97	1.56	3.65	7.71	7.06	−0.295	2.67	0.89	3.42	9.34	1.63	−0.67	−0.23
Platichthys flesus	Kändler and Thurow, 1959	6.18	−1.11	1.55	−0.07	2.20	8.38	6.51	−1.02	1.78	0.07	2.47	8.86	0.48	0.14	0.27
Limanda limanda	Kändler and Thurow, 1959	5.17	0.215	2.23	1.08	2.78	6.27	5.48	−0.550	1.94	0.37	2.52	7.93	1.66	−0.71	−0.26
Microstomus pacificus	Hagerman, 1952	5.20	0.386	2.39	1.26	2.94	6.20	5.92	−0.0769	2.18	0.92	2.81	6.97	0.77	−0.34	−0.13
Microstomus kitt	Rae, 1948	5.64	−0.112	1.91	0.83	2.51	6.20	6.04	−0.591	1.66	0.42	2.30	6.94	0.74	−0.41	−0.21
Glyptocephalus cynoglossus	Bowers, 1959	5.18	−0.0715	2.01	0.80	2.56	6.49	4.99	0.152	2.06	0.99	2.59	5.90	−0.59	0.19	0.03
Pleuronectes platessa	Petersen, 1922	4.38	−0.128	1.51	0.61	1.97	5.02	4.70	−0.333	1.49	0.46	1.99	5.65	0.63	−0.15	0.02
Hippoglossoides platessoides	Bagenal, 1955	2.86	0.451	1.62	0.93	1.92	3.65	4.14	0.486	2.05	1.18	2.49	4.83	1.18	0.25	0.57
Gobius paganellus	Miller, 1961	1.82	0.418	1.04	0.72	1.23	1.88	1.79	0.343	0.970	0.64	1.16	1.92	0.04	−0.08	−0.07
Callionymus lyra	Chang, 1951	3.30	−0.237	1.75	0.32	2.10	6.57	3.04	0.470	1.79	0.98	2.11	4.17	−2.40	0.66	0.01
Roccus lineatus	Scofield, 1931	6.83	−0.293	2.55	0.85	3.27	8.93	7.61	−1.15	2.25	0.13	3.05	10.8	1.84	−0.72	−0.22
Amphisticus argenteus	Carlisle, 1960	5.46	−0.407	1.92	0.51	2.50	7.34	5.91	−0.699	1.87	0.29	2.49	8.12	0.78	−0.22	−0.01
Leuresthes tenuis	Clark, 1925	2.94	0.940	2.07	1.43	2.38	3.51	3.22	0.788	2.02	1.33	2.36	3.80	0.29	−0.10	−0.02
Anoplopoma fimbria	Pruter, 1954	7.40	−0.288	2.37	0.95	3.15	8.12	7.67	−0.647	2.16	0.64	2.97	8.60	0.48	−0.31	−0.18
Scorpaenichthys marmoratus	O'Connell, 1953	7.40	0.506	3.17	1.75	3.95	8.12	7.72	0.440	3.16	1.74	3.98	8.27	0.15	−0.01	0.03



APP. FIG. 11. The ratio between the catabolic rates of males and females of the same species, plotted against the corresponding ratios of asymptotic size. Log scale. App. XI.

Notice, that in the analysis of interspecific differences (App. X) it was found that asymptotic size of a species is determined by H exclusively, whereas in the comparison of males and females of the same species the present analysis indicates dependence of asymptotic size upon *k* only.

APP. XII. NATURAL MORTALITY AND ASYMPTOTIC SIZE IN VARIOUS FISHES

ESTIMATES OF M AND μ

Equation E2 gives the dependence of natural mortality, M, upon body size and the parameters of anabolism and catabolism as

$$M = \mu \left(\frac{1+\alpha}{1-\alpha} H\, w^{m-1} + k\, w^{n-1} \right) \qquad .....(E2).$$

Data on growth and natural mortality in a number of fish species were published by Beverton and Holt (1959, Table I). They listed L_∞ cm, $k/3$ years^{-1} and M years^{-1} (App. Table VII of

APP. TABLE VII. Parameters of growth and natural mortality in various fishes. Adapted from Beverton and Holt (1959, Table I).

Species	$ln\ {}_1W_\infty$	$ln\ {}_1k$	M years^{-1}	$ln\ {}_nW_\infty$
Clupea harengus	5.49	0.13	0.25	5.86
Clupea harengus	4.41	0.67	0.78	4.75
Clupea pallasii	4.71	−0.14	0.56	5.06
Sardinops coerulea	5.07	0.16	0.15	5.43
Gadus callarias	9.93	−0.51	0.2	10.44
Gadus minutus, males	4.29	0.23	1.1	4.63
Gadus minutus, females	4.83	0.18	0.9	5.18
Gadus virens	9.30	−0.56	0.15	9.79
Merluccius merluccius, males	6.63	−0.94	0.6	7.04
Merluccius merluccius, females	7.56	−1.20	0.5	8.00
Pleuronectes platessa, males	6.72	−0.80	0.22	7.13
Pleuronectes platessa, females	8.04	−1.43	0.12	8.49
Pseudopleuronectes americanus	6.63	0.18	0.3	7.04
Solea vulgaris	6.27	0.18	0.25	6.67
Acipenser fulvescens	10.83	−1.90	0.01	11.36
Acipenser medirostris *Acipenser transmontanus*	12.39	−1.71	0.03	12.97
Blennius pholis	3.78	−0.11	0.9	4.10
Callionymus lyra, males	4.95	0.25	0.96	5.31
Callionymus lyra, females	3.87	0.50	0.86	4.20
Cottus gobio, males	1.20	0.74	1.1	1.45
Cottus gobio, females	1.26	0.18	0.9	1.51
Cottus gobio, males	0.90	0.99	0.9	1.14
Cottus gobio, females	0.90	0.41	0.8	1.14
Phoxinus phoxinus	1.89	0.50	1.1	2.16
Gasterosteus aculeatus	0.99	0.65	0.9	1.23
Gasterosteus pungitius	−0.33	1.76	1.1	−0.13
Cynoscion macdonaldi	9.84	−0.11	0.3	10.35
Perca fluviatilis	5.49	−0.51	0.29	5.86
Perca fluviatilis	5.88	−0.94	0.16	6.27
Stizostedion canadensis	6.36	−0.87	0.44	6.76
Dasyatis akajei, females	10.32	−1.20	0.4	10.84
Pneumatophorus diego	6.36	0.18	0.9	6.76
Neothunnus macropterus	11.04	0.41	0.8	11.58

the present paper). M was estimated independently of the growth parameters, which were computed by means of equation A23, thus putting $n = 1$ and $m = 2/3$. In order to adapt the estimates to the present model L_∞ was turned into W_∞ by assuming $W_\infty = q L_\infty^3$, $q = 0.009$. The mean size, $\hat{w}$, of the fish from which the parameter estimates were made was assumed to be determined by

$$ln\ \hat{w} = 0.92\ ln\ {}_1W_\infty - 0.92 \qquad \ldots\ldots(11\text{-}1)$$

which is the empirical relationship estimated from App. Table V. As in the preceding examples, ${}_1W_\infty$ designates the estimate of W_∞ obtained for $m = 2/3$ and $n = 1$. The relationship between ${}_nW_\infty$ and ${}_1W_\infty$ is given by equation 9-8. The estimates, $m = 0.56$ and $n = 0.83$, made in App. X give

$$ln\ {}_1W_\infty = 1.23\ ln\ {}_nW_\infty - 0.23\ ln\ \hat{w} \qquad \ldots\ldots(11\text{-}2).$$

Inserting 11-1 into 11-2 and rearranging leads to

$$ln\ {}_nW_\infty = 0.97\ ln\ {}_1W_\infty - 0.20 \qquad \ldots\ldots(11\text{-}3).$$

The values of $ln\ {}_nW_\infty$ of App. Table VII were computed by means of 11-3.

Equation 11-3 into 11-1 and rearranging gives

$$ln\ \hat{w} = 0.89\ ln\ {}_nW_\infty - 1.10 \quad \text{or} \quad \hat{w} = {}_nW_\infty{}^{0.89}/3.00 \qquad \ldots\ldots(11\text{-}4).$$

By means of equation A19, written in the form

$${}_nH = {}_nk\ {}_nW_\infty^{n-m}$$

and substituting $\hat{w}$ for w, equation E2 can be expressed as

$$M/\mu = \frac{1+\alpha}{1-\alpha}\ {}_nk\ {}_nW_\infty^{n-m}\ \hat{w}^{m-1} + {}_nk\ \hat{w}^{n-1} \qquad \ldots\ldots(11\text{-}5).$$

Inserting the following values of the parameters:

$\alpha = 0.8$ (as estimated for plaice in App. VII)

$ln\ {}_n\bar{k} = ln\ {}_nk = 0.9$; ${}_nk = 2.5$ (average for 81 species, App. X)

$n = 0.83$; $m = 0.56$ (also from App. X)

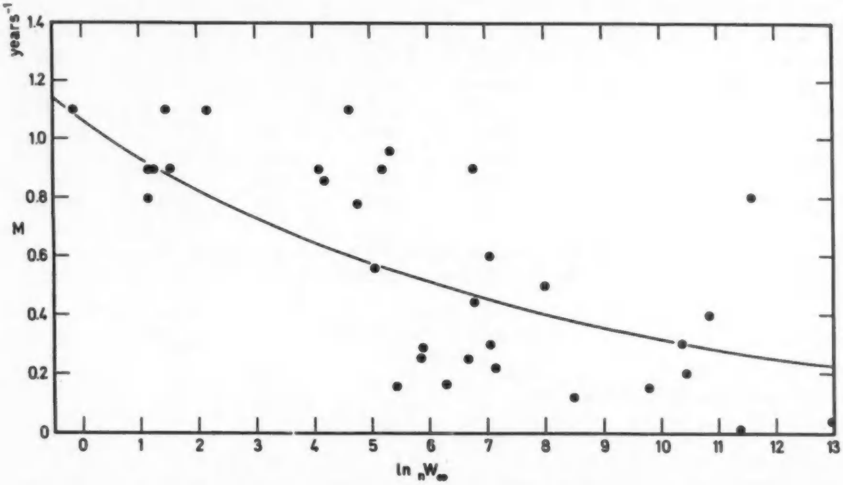
gives, after insertion of 11-4

$$M/\mu = 36.5\ {}_nW_\infty^{-0.122} + 3.02\ {}_nW_\infty^{-0.151} \qquad \ldots\ldots(11\text{-}6).$$

Inserting a range of values of asymptotic size provides a set of figures proportional with natural mortality (disregard the third column for the moment):

$ln\ {}_nW_\infty$	M/μ years^{-1}	M years^{-1}
0	39.53	1.07
2	30.85	0.83
4	24.10	0.65
6	18.82	0.51
8	14.70	0.40
10	11.47	0.31
12	8.96	0.24
14	7.00	0.19

So far, the data in App. Table VII have not been used at all. As there is no independent means of estimating the proportionality factor, μ, the analysis cannot be carried through without the use of fresh data. After a few trials it was found that the value $\mu = 0.027$ distributes the 33 individual observations of App. Table VII with about equal numbers on either side of the curve (16 above, 17 below). It was therefore adopted and used in computing the estimates of M in the third column above. The observations are plotted and the curve drawn in App. Fig. 12. The agreement is fair enough so that the evidence of available material does not reject the hypothesis on the relationship between metabolic rates and natural mortality laid down in equation E2. The model implies that the smaller of the two sexes (usually the male) has the higher mortality, as is often observed (e.g. Beverton and Holt, 1959).



APP. FIG. 12. The instantaneous coefficient, M, of natural mortality as a function of asymptotic size in fishes. Each entry represents one species (data from App. Table VII). The regression line is computed by means of the model by inserting parameter estimates made in previous examples into equation E2. App. XII.

Mortality due to predation probably operates in almost the same way as mortality due to metabolic activities and is perhaps quite considerable. The value of μ used above is therefore likely to be an overestimate. It should preferably be determined in studies of carefully protected populations with predation nil or constant.

The present knowledge of actual parameter values indicates that equation E2,

$$M/\mu = \frac{1+\alpha}{1-\alpha} H\, w^{m-1} + k\, w^{n-1}$$

can be simplified without introducing serious bias. Parameter estimates made in various examples indicate that likely values are:

$$k \approx 1;\ 1 < H < 10^2;\ \frac{1+\alpha}{1-\alpha} \approx 10$$

$$m \approx 2/3;\ n \approx 5/6$$

where H is an increasing function of asymptotic size, as indicated by equation A19. Consider two fish species of extreme asymptotic sizes, 10^{-1} g and 10^{6} g. Let them be hatched weighing 10^{-4} g and 10^{-3} g, respectively. The H value for the small species will be about 1 and for the big one it is not over 10^{2}. We then have

The small species				The big species			
$M/\mu = 10\,w^{-1/3} + w^{-1/6}$				$M/\mu = 1000\,w^{-1/3} + w^{-1/6}$			
w (g)	$10\,w^{-1/3}$	$w^{-1/6}$	M/μ years^{-1}	w (g)	$1000\,w^{-1/3}$	$w^{-1/6}$	M/μ years^{-1}
10^{-4}	220	5	225	10^{-3}	10,000	3	10,003
10^{-3}	100	3	103	1	1,000	1	1,001
10^{-2}	50	2	52	10^{3}	100	0.3	100.3
10^{-1}	20	2	22	10^{6}	10	0.1	10.1

Thus, neglecting the second term of equation E2 is of no consequence for big species and leads to an overestimate of 10% for fully grown specimens of very small species. We can put

$$M = \mu \frac{1+\alpha}{1-\alpha} H \; w^{m-1}$$

which can be further simplified to

$$M = \mu' \, w^{m-1}.$$

Here, however, the proportionality constant, μ', is a function of W_∞. Putting $m = 2/3$ gives that natural mortality is roughly inversely proportional with the cube root of weight:

$$M = \mu'/w^{1/3}.$$

Take North Sea plaice as an example. The natural mortality was estimated by Beverton (Beverton and Holt, 1959, p. 151) as 0.22 years^{-1} for males and 0.12 years^{-1} for females. Averaging and assuming that the mean weight of the fish investigated was about 500 g, we have $M = 0.17$, $w^{-1/3} = 0.125$. The following table can be set up:

w (g)	$w^{-1/3}$	M years^{-1}	Mortality (%)	
10^{-3}	10.0	13.5	3.6 per day	
10^{-2}	4.64	6.26	1.6 per day	
10^{-1}	2.15	2.90	22 per month	
1	1.00	1.35	11 per month	
10	0.464	0.626	5.1 per month	
10^{2}	0.215	0.290	25 per year	
10^{3}	0.100	0.135	13 per year	
10^{4}	0.0464	0.0626	6.1 per year	
500	0.126	0.17	16 per year	$\mu' = 1.35$

If it does at all make sense to assume that the anabolic parameters are constant through the whole life of the fish, we find that larval mortality amounts to a few per cent per day, and that the recently settled bottom stages have a mortality of 20–30% per month. Both of these figures seem reasonable enough. The table also discloses a useful rule of thumb: for species of the size order $W_\infty = 10^3$ g we have

$$M = w^{-1/3}$$

and also, that when the weight is multiplied by 10 the natural mortality is halved.

APP. XIII. GROWTH OF *LEBISTES RETICULATUS*

Most growth data for fishes refer to medium-sized species, so that it was thought valuable to investigate an extreme case in some detail. The smallest easily kept species available was the guppy, *Lebistes reticulatus*, a stock of which was obtained from the Botanical Gardens of Copenhagen by the courtesy of the chief gardener, Mr Nilaus Jensen. They were primitive and uniform guppies which had not been mixed with other populations for many years. Mr Christian Frandsen conducted the growth experiments with great care and pet shop equipment.

When choosing *Lebistes* I was not aware that objections to the use of a cyprinodont fish for the purpose can be made. Various attempts to determine the power n of the catabolic term, $k\ w^n$, in cyprinodonts have given low values, $n = 2/3$, which seem to be unique in the animal kingdom (see Winberg, 1956, 1961; Paloheimo and Dickie, 1966a). Whether this is due to some unknown physiological difference between cyprinodonts and other fishes or is the effect of some bias or other, it is likely to show up somewhere in the present work.

The experiments fall into two groups, one in which the fish were reared separately at room temperature and another in which they were reared in groups at a range of temperatures. When the growth experiments had come to an end the surviving males were used for fasting experiments (see App. VIII). Some results of the fasting are utilized directly in the present example.

SINGLE SPECIMENS AT ROOM TEMPERATURE

ESTIMATES OF k AND m

In each of two experiments 12 new-born *Lebistes* were placed in 1.5-liter glass jars, one in each jar, at room temperature. Once every day, except on Sundays, they were fed commercial dry fish food in surplus, the surplus being removed by snails. The water was changed every 3 months. The temperature was read daily, except on Sundays. The fish were measured once a week in the first months and at longer intervals later on. Measurements were made from the tip of the nose to the tip of the tail, in units of 0.02 cm. After 406 days in the first experiment, and after 365 days in the second one, the surviving fish were kept fasting for about 3 weeks. In this period the water was renewed and the jar cleaned every 2nd day. At the same time the fish were weighed with an accuracy of 0.0001 g, the fourth decimal apparently being useless because of differences in the amount of water adhering to the skin. In the first experiment the fish were fed again afterwards and the fasting repeated, so that duplicate determinations became available.

The temperature oscillated irregularly between 19 and 23 C and was usually about 21 C. Most of the time the fish were exposed to natural daylight and dark, but towards the end of the experiment they were moved to a darkened room with artificial light 14 hr per day. Linear regression analyses were made with the growth rate as the dependent variable and with body length, temperature, and hours of daylight as independent variables. The inclusion of temperature or daylight, or both, often reduced the variance, but never significantly, not even when several sets of data were pooled. Therefore no further attention was paid to these variables, the mean temperature being about 20.5 C and the mean day length about 12 hr.

In the second experiment the fish for no apparent reason grew very little in the first months. In both experiments the females were virgin.

Since growth curves for single fish are scarce in literature, the length measurements of the 12 *Lebistes* from the first and more successful experiment are given in App. Table VIII. First, we shall test Pütter's approximation:

$$\frac{dw}{dt} = {}_1\mathrm{H}w^{2/3} - {}_1kw \quad \text{or} \quad \frac{dl}{dt} = {}_1\mathrm{E} - \frac{{}_1k}{3}l \quad \ldots\ldots(1),\ (\mathrm{A}23)$$

using, as before, the suffix 1 to distinguish the Pütter parameters. Fitting length increments versus length (adults only) to a straight line produced 11 estimates of $ln\ {}_1k$ from the first experiment (App. Table VIII, omitting one fish in which sex reversal was observed). Fasting experiments

App. Table VIII. Growth in length of 12 *Lebistes* reared separately in 1.5 liter jars. The measurement is given in italics the first time the sex could be determined. When 30 weeks old, fish No. 3 apparently changed from female to male. Measurements were to nearest unit below (f, female; m, male). Length in units of 0.02 cm.

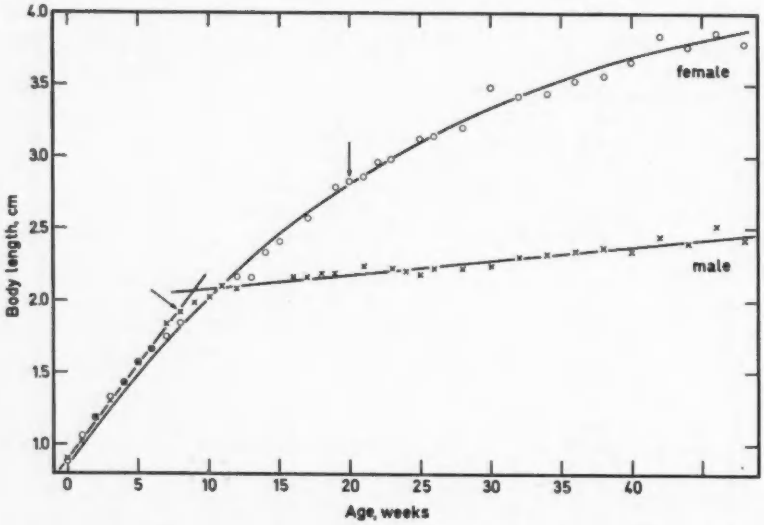
Age (weeks)	Length											
	1 f	2 m	3 fm	4 f	5 m	6 f	7 f	8 m	9 f	10 f	11 m	12 f
0	46	45	46	47	46	43	44	46	43	43	40	43
1	53	51	52	55	53	50	53	49	51	48	49	50
2	60	59	60	66	60	58	59	58		56	54	58
3	64	65	62	73	64	63	66	65	62	66	61	69
4	72	71	69	81	71	66	71	73	67	70	67	74
5	79	78	77	87	79		78	83	76	74	71	79
6	85	83	83	94	84		83	89	84	81	73	83
7	*91*	92	*89*	*106*	*90*		87	101	89			
8	101	*96*	98	110	93	81	92	*105*	*95*			
9	107	99	105	120	97	84						
10	113	101	111	124	100	90				103	84	97
11	116	105	116	128	103	96				107	89	99
12	121	104	121	133	104		108	111	112	112	93	*106*
13							108	113	116	117	95	110
14						112	116	115	120	118	97	
15						118	120	117	123	121	99	119
16	132	108	133	150	108	121						123
17	134	108	133	151	107	*126*	128	120	135	*130*	*101*	133
18	137	109	136	152	107	128			143	132	104	136
19	139	109	136	158	108		139	118	146	133	101	140
20							*141*	118	149	138	102	140
21	142	112	142	161	109	137	143	118	149	139	108	144
22						141	148	119	150			
23	151	111	141	170	113	143	149	118		148	106	151
24	155	110	141	171	116					152	105	157
25	159	109	140	173	112	151	156	121	154	148	106	157
26	162	111	140	175	112		157	121	157	151	107	159
28	167	111	139	176	111		160	121	164	158	106	165
30	176	112	*140*	192	112	163	174	121	171	161	106	169
32	179	115	143	197	112	168	171	121	170	167	106	171
34	181	116	142	204	114	176	172	123	177	173	109	174
36	192	117	143	209	114	187	176	128	179	174	110	174
38	192	118	145	216	114	188	178	128	181	180	113	176
40	192	117	144	216	115	191	183	126	186	197	113	181
42	198	122	149	218	116	196	192	131	199	196	110	177
44	203	120	148	223	116		188	131	201	198	113	179
46	212	126	153	227	123		193	136	206	201	116	181
48	213	121	149	221	118		189	135	210			
50	215	123	150	223	118							
52	216	124	152	221	123					205	117	
54								134	215			
58	218	124	155		121							

(see App. VIII) produced estimates of $ln\ {}_1k$ for 14 fish from both experiments. In neither case the difference between males and females was significant. The data are:

	df	$\overline{ln\ {}_1k}$	$s^2\{y\|x\}$	$ln\ \overline{{}_1k} = \overline{ln\ {}_1k} + (s^2\{y\|x\}/2)$	$\overline{{}_1k}$
Growth	11	1.73	0.396	1.93	6.89
Fasting	13	1.04	0.0625	1.08	2.93

where df is the number of degrees of freedom and where y stands for increment and x for length. Means and variances differ significantly so that the physiological interpretation of equation 1 must be rejected if the data are reliable. The inclusion of growth data from the second experiment does not change the picture, but since the juvenile growth in that experiment was abnormal it was considered safer to use these fish for the final fasting experiment only.

Empirically, the rejected equation gives a nice enough fit to data, for females at least, as examplified in App. Fig. 13 in which is shown a growth curve of a female (App. Table VIII, No. 7) fitted to equation 1 by the aid of equation A27; it is based on both juvenile and adult growth. The growth of juvenile males does not differ significantly from that of juvenile females, but with the onset of maturity the male curves change abruptly (see App. Fig. 13). The entire male curve gives a poor fit to equation 1 and is better described by two straight lines, one for juveniles and another for adults. Fits of equation 1 to each of the two parts of the male growth curve separately is technically quite possible but leaves the parameter values more or less accidental.



APP. FIG. 13. *Lebistes*. Growth curves of one male and one female (from App. Table VIII, fish No. 2 and 7). Arrows indicate when the sex was first recognized. Female data are fitted to equation A27. App. XIII.

The parameters m and n of the generalized growth equation,

$$\frac{dw}{dt} = \mathrm{H}\ w^{m} - k\ w^{n} \quad \text{or} \quad \frac{dl}{dt} = \mathrm{E}\ l^{3m-2} - \mathrm{K}\ l^{3n-2} \ldots\ldots \text{(B18), (A18)}$$

were in App. X estimated as $m = 0.56$, $n = 0.83$. These values based on a large number of species were found to stabilize k on the level indicated by fasting experiments (App. IX) on several species. If the above values of m and n are applicable to *Lebistes* a plot of $(dl/dt)\ l^{2-3m}$ against $l^{3(n-m)}$ should give a value of k (i.e. of ${}_{.83}k$) which is not significantly different from a similar estimate from weight loss data for fasting animals. In the same way as above we get

	df	$ln\ {}_{.83}k$	$s^2\{y\mid x\}$	$ln\ \overline{{}_{.83}k}$	$\overline{{}_{.83}k}$
Growth	11	1.47	0.347	1.64	5.17
Fasting	13	0.803	0.221	1.02	2.79

The difference between the two estimates of k is smaller than for $m = 2/3$, $n = 1$. Yet, the difference is significant and the hypothesis $m = 0.56$, $n = 0.83$, must be rejected, too.

There is no means of estimating independently both m and n from the *Lebistes* data. This, I think, could be done only by means of respiration data for animals of different size, i.e. from experiments like those Saunders (1963) made on cod (see App. IV). *Lebistes*, however, would present extreme difficulties because of the short size range covered by the species: birth, 10^{-2} g; first maturity, 10^{-1} g; asymptotic size, males 10^{-1} g, females 1 g. The short size range, however, with the small deviation from unit weight gives the advantage that an error in the estimate of n influences only slightly the estimates of other parameters. Notice the reasonably small differences of the estimates of ${}_{1}k$ and ${}_{.83}k$ above. Thus, sticking to Pütter's n ($= 1$) is likely to lead to useful although somewhat biased estimates of other parameters.

Another problem is that the reason why the hypotheses regarding m and n must be rejected is unknown. It may be that the two sets of values tested just don't apply to *Lebistes*. However, it is also possible that the assumptions underlying the estimation of k from fasting experiments do not hold. For instance, the chemical composition of the body may have changed during the fasting experiments, or the behaviour of fasting *Lebistes* may have differed significantly from that of fed ones (although no such difference was observed). Accepting the fasting estimate of k presents the more interesting possibilities for further analysis, and this, admittedly, is the reason why it has been done below.

Having thus defined $n = 1$, and k equal to the value of k obtained from fasting experiments we are landed with the following variety of equation A18:

$$ln\left(\frac{dl}{dt} + \frac{k}{3}\ l\right) = ln\ \mathrm{E} + (3m-2)\ ln\ l \qquad \ldots\ldots(12\text{-}1)$$

which is linear with slope 3m–2. Eleven estimates of m from growth data for males and females from the first experiment have a mean value of 0.500 with a 95% confidence interval of ±0.078. The mean is not significantly different from the estimate, $m = 0.561$, based on growth data for 81 species (App. X). Inserting $m = 1/2$ in equation 12-1 leads to the growth equation

$$\frac{dl}{dt} = \mathrm{E}\ l^{-1/2} - \mathrm{K}\ l$$

$$\mathrm{E} = \frac{\mathrm{H}}{3q^{1/2}};\ \mathrm{K} = \frac{k}{3} \qquad \ldots\ldots(12\text{-}2)$$

which shall be further investigated in the next paragraph.

Growth Rates at Different Temperatures

ESTIMATES OF k, p_k, H, $\mathrm{H}a$, $\mathrm{H}b$, $\mathrm{H}p_0$, $\mathrm{H}p_2$, τ_m, W_∞, $\tau_{\infty m}$, $W_{\infty m}$ AND τ_{mg}

New-born *Lebistes*, most of them born at room temperature, were placed in 39 6-liter glass jars, about 15 in each jar. The jars were aerated and many of them heated electrically. The treatment of the fish was the same as in the experiments with single specimens (see above). The mortality was generally low. Quite often, some few died in the 1st week, but afterwards, the mortality was low and sometimes nil until some accident (e.g. break-down of the temperature regulation) occurred. Whenever mortality had occurred, the corresponding observation of increment was discarded. Still, the whole curve is biased if the fish which died had other growth parameters than the survivors. Most series were carried through the 1st year of life and some up to 500 days. In the end, the males were kept fasting for about 3 weeks (see App. VIII). Females could not be used in fasting experiments because of interfering cyclic weight changes.

Most jars were kept in a room with no daylight but artificially illuminated 14 hr of the day. The temperature oscillated 1 C, occasionally 2 C, on either side of the mean. Within experiments, however, there was no significant dependence of growth rate upon temperature, or upon day length in the few series which were not artificially illuminated.

ESTIMATING THE COEFFICIENT OF FASTING CATABOLISM, k

An appropriate although to some extent arbitrary growth equation for *Lebistes* was derived above (equation 12-2) which on rearrangement becomes

$$\frac{dl}{dt}\, l^{1/2} = \mathrm{E} - \mathrm{K}\, l^{3/2} \qquad \ldots\ldots(12\text{-}2)$$

from which K can be determined as the slope of a straight line. The corresponding estimate of E is of little interest because K and E are heavily correlated when estimated from the same straight line. The fish in three of the original 39 jars died so early that they cannot be used for estimation of adult fish parameters. Thus 36 estimates of K are available for each sex. The variance of K varies significantly from one series to another, major influences apparently being the number of observations, the general smoothness of the growth curve, and the size range between the first and the last observation, this latter being quite a problem with males which sometimes grew less than 1 mm from the sex became distinguishable until the end of the experiment. Five estimates of K for males and another five for females were discarded because the variances were conspicuously higher than in the remaining 31 experiments. The 95% confidence interval of K in many cases included zero, particularly for males. The estimates of k (= 3K) and their variances are listed in App. Table IX. k (in terms of years^{-1}) is plotted against temperature in App. Fig. 14. Log scales were not used because there are a few negative values for males. Direct comparison with App. Fig. 7 (App. VIII), which gives the corresponding relationship for fasting experiments with males, is not possible, but the regression line from App. Fig. 7 has been entered in App. Fig. 14. It is obvious that we cannot reject the hypothesis that the quantities k, as estimated from fasting experiments and from growth experiments, are the same. The experiments, however, are not satisfactory because as already explained it resulted that females, except virgin ones, are unsuitable for fasting experiments and males are unsuitable for growth experiments. Some very high entries for males (App. Fig. 14) leap into the eye. They are probably biased by including observations of juvenile growth. After all, the definition of a juvenile *Lebistes* as one in which the sex cannot be determined by inspection is rather arbitrary. Even for females the variance about the regression line is very high. Application of equation C6 to female data gives an estimate of the 95% confidence interval of the temperature coefficient,

$$p_k = 0.0848 \pm 0.0971$$

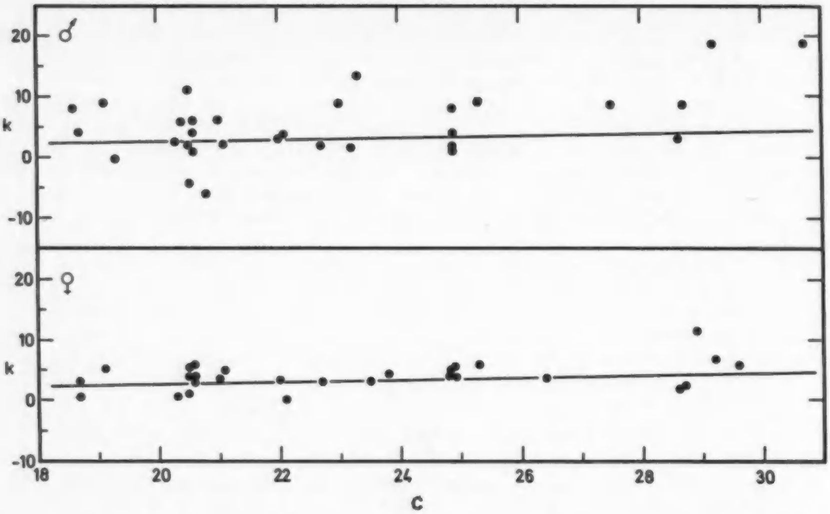
so that the hypothesis $p_k = 0$ cannot be rejected.

App. Table IX. *Lebistes reticulatus*. Values of k and their variance estimated from growth data by means of equation 12-2. Estimates discarded owing to a conspicuously high variance are in italics. Adults only (App. XIII, cf. App. Fig. 14).

Temp τ (C)	Males $k = 3K$ (years^{-1})	Males s_k^2	Females $k = 3K$ (years^{-1})	Females s_k^2
18.6	8.15	24.6	3.20	3.02
18.7	4.49	22.5	0.547	4.54
19.1	9.01	14.3	5.62	6.11
19.3	−0.485	10.0	*7.71*	52.5
20.3	2.68	9.45	0.391	0.728
20.4	5.78	16.3	6.23	2.75
20.5	11.2	11.1	5.39	0.471
20.5	−4.59	34.2	0.885	7.52
20.5	*3.75*	136	4.18	0.891
20.5	2.35	2.40	4.41	0.773
20.6	5.93	33.7	3.66	1.60
20.6	3.97	1.93	2.90	0.238
20.6	0.919	6.11	3.90	2.02
20.8	−6.08	21.1	3.71	1.30
21.0	6.20	17.0	3.45	2.71
21.1	2.13	4.93	5.19	0.816
22.0	3.02	9.32	3.43	1.01
22.1	3.59	33.1	0.142	3.76
22.3	*12.4*	96.8	*−3.35*	19.1
22.7	2.02	20.2	3.25	5.61
23.5	9.07	9.58	2.98	0.979
23.7	1.38	33.0	*6.63*	31.0
23.8	13.7	13.4	4.79	0.588
24.9	1.22	4.53	4.11	0.816
24.9	1.83	4.97	4.80	5.69
24.9	4.29	6.05	4.23	2.78
24.9	2.22	15.0	5.34	7.36
25.3	9.55	10.6	6.15	1.64
26.4	*−9.88*	121	4.45	8.03
27.5	8.72	10.5	*11.0*	33.8
28.6	3.00	3.82	1.90	3.42
28.7	9.75	4.12	2.64	1.49
28.9	*4.57*	119	11.6	7.20
29.2	18.5	25.8	7.25	2.90
29.6	*21.2*	93.6	5.71	1.01
30.7	18.1	31.1	*8.00*	118

ESTIMATING THE COEFFICIENT OF NET ANABOLISM, H

Since there is no evidence to the contrary, it can be assumed for the present that k is the same in male and female *Lebistes*. k of juveniles is not known at all, but we shall make the simple as-



App. Fig. 14. *Lebistes*. Values of $_1k$ estimated from growth data. The regression lines are reproduced from App. Fig. 7 which gives similar data (log scale, however) for fasting experiments. App. XIII.

sumption that it is the same as in adults. Thus, the entire variation of the growth curve with sex and developmental stage is placed upon E of equation 12-2 so that E can be estimated from

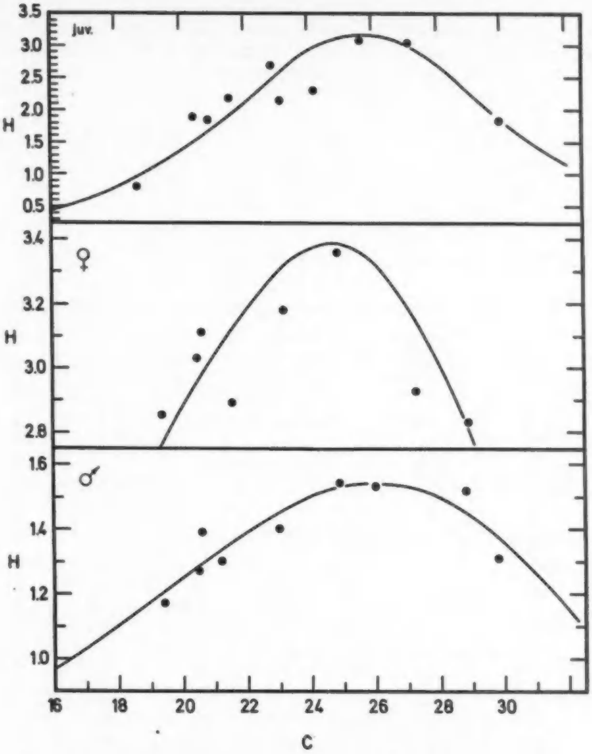
$$E = \frac{dl}{dt}\, l^{1/2} + K\, l^{3/2}.$$

To avoid artificial correlation of E and K, the estimate of k made in App. VII:

$$K = k/3 = 3.24\ e^{0.0476\ \tau}$$

must be inserted. The computation of $H = 3\ E\ q^{1/2}$ requires estimates of $q = w/l^3$. Plausible values of q were found to be 0.010 for females, 0.009 for juveniles, and 0.008 for males. Insertion of the appropriate value of k gives for each experiment a number of estimates of E, one for each observation of growth rate, dl/dt, and length, l. The means of these estimates for each experiment were arranged according to temperature and pooled within short temperature ranges to make the presentation clearer. Thus the following results were obtained (see App. Fig. 15):

Females				Males			
τ (C)	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{H}$ (years g$^{-1/2}$)	τ (C)	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{H}$ (years g$^{-1/2}$)
19.4	9.50	2.85	0.351	19.4	3.59	1.17	0.855
20.5	10.1	3.03	0.330	20.5	3.89	1.27	0.787
20.6	10.4	3.11	0.322	20.6	4.24	1.39	0.719
21.6	9.62	2.89	0.346	21.2	3.99	1.30	0.769
23.2	10.6	3.18	0.314	23.0	4.29	1.40	0.714
24.9	11.2	3.36	0.298	24.9	4.72	1.54	0.649
27.3	9.75	2.93	0.341	26.0	4.69	1.53	0.654
29.6	9.45	2.83	0.353	28.7	4.66	1.52	0.658
				29.8	4.00	1.31	0.763



App. Fig. 15. *Lebistes*. The coefficient, H, of net anabolism plotted against temperature and fitted to the reciprocal of equation C4. H is determined from growth data, using the approximation $dw/dt = \mathrm{H}\, w^{1/2} - k\, w$. App. XIII.

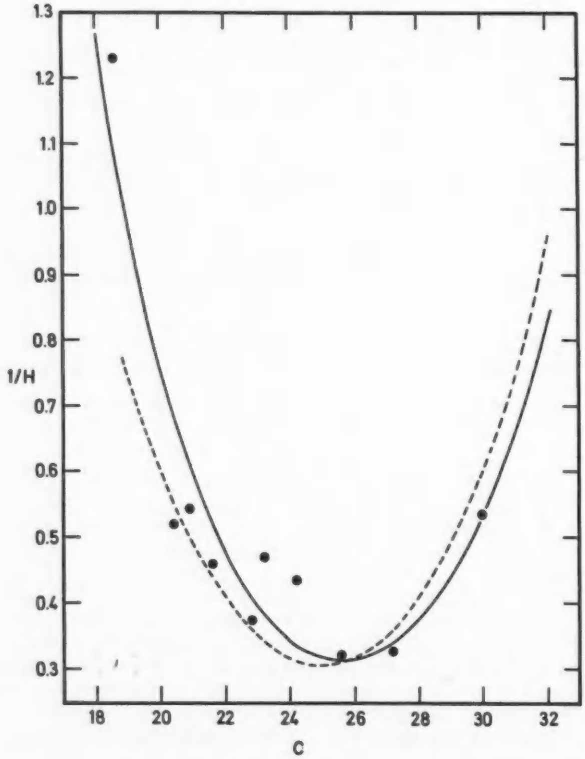
For juveniles, corresponding data were obtained in a slightly different way to avoid irregularities during the first time after birth and when sexual maturity is approaching. From plots of length against age was read the time to grow from a length of 1.2 cm to 1.4 cm (dt/dl, measured in days per 0.2 cm). The mean temperature in the period concerned was computed and the data arranged according to temperature. dt/dl was converted to dl/dt expressed in cm per year, and mean values of temperature and dl/dt computed for groups of four observations, each group covering a short temperature range. E and, hence, H then could be estimated as above (see App. Fig. 15 and 16)

τ (C)	$\frac{dl}{dt}$ (cm years^{-1})	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{\mathrm{H}}$ (years g$^{-1/2}$)
18.6	2.73	4.40	0.812	1.23
20.4	4.69	6.75	1.92	0.521
20.9	4.41	6.46	1.84	0.543
21.6	5.40	7.64	2.18	0.459

(*Continued*)

(*Concluded*)

τ (C)	$\frac{dl}{dt}$ (cm years^{-1})	E (cm$^{3/2}$ years^{-1})	H (g$^{1/2}$ years^{-1})	$\frac{1}{H}$ (years g$^{-1/2}$)
22.8	6.88	9.41	2.68	0.373
23.2	5.18	7.49	2.13	0.469
24.2	5.61	8.07	2.30	0.435
25.6	7.98	10.90	3.11	0.322
27.2	7.75	10.76	3.07	0.326
30.0	3.83	6.56	1.87	0.535



App. Fig. 16. *Lebistes*. 1/H (see App. Fig. 15) for juveniles, plotted against temperature and fitted to equation C4. The dotted line was made by fitting data given by Gibson and Hirst to a catenary curve. App. XIII.

The relevant parameters are given by

$$\frac{1}{H} = a\, e^{p_0 \tau} + b\, e^{p_2 \tau} \qquad \ldots\ldots(C4).$$

Rough estimates of the four parameters, a, b, p_0 and p_2, can be made as in App. III by reading off four values from eye-fitted curves through the observations. For instance, putting $T = \tau/3.75$, $A = e^{3.75\ p_0}$ and $B = e^{3.75\ p_2}$, and reading off such a curve for males at T = 5, 6, 7, 8 gave

τ	T	H	$\frac{1}{H}$
18.75	5	1.16	$0.862 = u = a\,A^5 + b\,B^5$
22.50	6	1.42	$0.704 = v = a\,A^6 + b\,B^6$
26.25	7	1.54	$0.649 = x = a\,A^7 + b\,B^7$
30.00	8	1.36	$0.735 = y = a\,A^8 + b\,B^8$

and, by simple arithmetics,

$$\left.\begin{matrix} A \\ \\ B \end{matrix}\right\} = \frac{(u\,y - v\,x) \pm \sqrt{(u\,y - v\,x)^2 - 4\,(u\,x - v^2)\,(v\,y - x^2)}}{2\,(u\,x - v^2)} = \left\{\begin{matrix} 2.0228 \\ \\ 0.7455 \end{matrix}\right.$$

$$A = e^{3.75\ p_0} = 2.0228 \qquad B = e =^{-3.75\ p_2} 0.7455$$

$$p_0 = 0.1879 \qquad p_2 = 0.07835$$

Simultaneous solution of two of the original four equations gives $a = 0.001419$ and $b = 3.5347$ so that

$$\frac{1}{H} = 0.00142\ e^{0.188\ \tau} + 3.53\ e^{-0.0784\ \tau}$$

for males.

Similarly, for females,

$$\frac{1}{H} = 0.000340\ e^{0.222\ \tau} + 1.77\ e^{-0.0856\ \tau}$$

and for juveniles,

$$\frac{1}{H} = 0.0000292\ e^{0.247\ \tau} + 185\ e^{-0.278\ \tau}.$$

Curves computed by means of the foregoing estimates are shown in App. Fig. 15 and 16. They fit the original points well enough; App. Fig. 15 shows plots of H against temperature; App. Fig. 16 is a plot of 1/H against temperature for juveniles and includes an independent estimate (from Ursin, 1963a, Fig. 8) based on the early growth of *Lebistes* reared by Gibson and Hirst. This second estimate is a fit to a catenary curve (equation C8) and is in reasonable accordance with the new result.

The maxima of the three curves of App. Fig. 15 are given by

$$\tau_m = \frac{ln\left(\frac{p_2}{p_0}\ \frac{b}{a}\right)}{p_0 + p_2} \qquad .....(C7)$$

as: juveniles 25.7 C, females 24.7 C, and males 26.1 C. It is not known whether the differences are significant or not.

ESTIMATING THE ASYMPTOTIC SIZE, W_∞ OR L_∞

The asymptotic weight as a function of temperature is given by equation C9 which for $m = 1/2$ and $n = 1$ becomes

$$W_\infty = [(ae^{p_0\tau} + b\ e^{-p_2\tau})\ k_0\ e^{p_k\tau}]^{-2} \qquad \ldots\ldots(12\text{-}3)$$

with maximum at temperature

$$\tau_{\infty m} = \frac{ln\left(\frac{p_2 - p_k}{p_0 + p_k}\frac{b}{a}\right)}{p_0 + p_2} \qquad \ldots\ldots(\text{C10}).$$

The letters p_2, p_0, b, and a refer to equation C4, i.e. they are anabolic parameters.

Converting weight to length by means of $w = q\ l^3$ and inserting the previously estimated parameter values in equations 12-3 and C10 provides points on the curves of App. Fig. 17 which shows L_∞ as a function of temperature for juveniles, females, and males. Maximum asymptotic size, $W_{\infty m}$, is reached at the following temperatures (equation C10) and with the values indicated (equation 12-3):

	$\tau_{\infty m}$ (C)	$W_{\infty m}$ (g)
Juveniles	25.0	0.768
Females	21.4	1.07
Males	21.7	0.204

Direct observation of L_∞ is impossible, but the length at the end of the growth experiment should be an underestimate of L_∞ for adults. Omitting series which did not survive 300 days we are left with 33 mean lengths of males and 32 of females. Pooling, as usual, over short ranges of temperatures provides the observations set out in App. Fig. 17. The hypotheses indicated by the curves obviously cannot be rejected by means of these observations. They are all situated below the curves, as they should be, and have roughly the right trend.

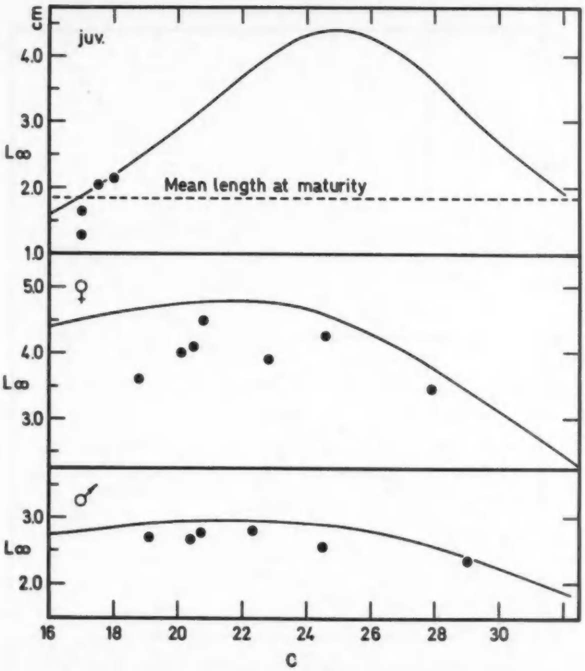
Juvenile L_∞ is usually purely hypothetical because the part of the curve effectuated before the onset of maturity is almost linear. Inspection of App. Fig. 17, however, shows that at low temperatures the juvenile L_∞ is considerably smaller than that of adults. If the estimates are correct it may even be smaller than the mean size at maturity which is 1.86 cm with a 95% confidence interval of 0.04 cm and no significant regression upon temperature. Thus, sexual maturity should not be reached at all below 17 C (see App. Fig. 17, juveniles) about which temperature the juvenile growth curve must be almost completed before the onset of maturity.

In fact, the fish in the four coldest jars developed growth curves as described. One is shown in App. Fig. 18. Arrows indicate when the first and the last fish could be identified to sex. At an age of about 175 days the juveniles seem to approach an asymptotic size of about 1.65 cm, but soon afterwards start growing rapidly, obviously with the parameters of the adults. These fish lived at temperatures about 18.8 C in the first 77 days and after the 287th day. When 78–286 days old (the interval concerning us here) they were kept at about 17 C. The "guesstimate" of $L_\infty = 1.65$ cm at 17 C is indicated on App. Fig. 17 and so are three other low-temperature observations. They are in good accordance with the expected values.

MAXIMUM GROWTH RATE AS A FUNCTION OF TEMPERATURE AND BODY SIZE

The growth equation with temperature incorporated can be expressed as

$$\frac{dw}{dt} = (a\ e^{p_0\tau} + b\ e^{-p_2\tau})^{-1}\ w^m - k_0\ e^{p_k\tau}\ w^n \qquad \ldots\ldots(\text{C11}).$$



App. Fig. 17. *Lebistes*. Estimated variation of asymptotic length, L_∞, with temperature. The observed lengths of males and females at the end of the growth experiment are indicated. On juveniles approaching L_∞ before becoming mature, see text. App. XIII.

Inserting the parameter values already found in the present Appendix with various values of τ and w produces curves like those in App. Fig. 19 which show the variation of male growth rate. The bigger the fish, the narrower the temperature interval within which it can grow. The negative growth rates indicate that a fish grown large at temperatures near $\tau_{\infty m} = 21.7$ C must loose weight when placed at extreme temperatures, even when fed their usual rations.

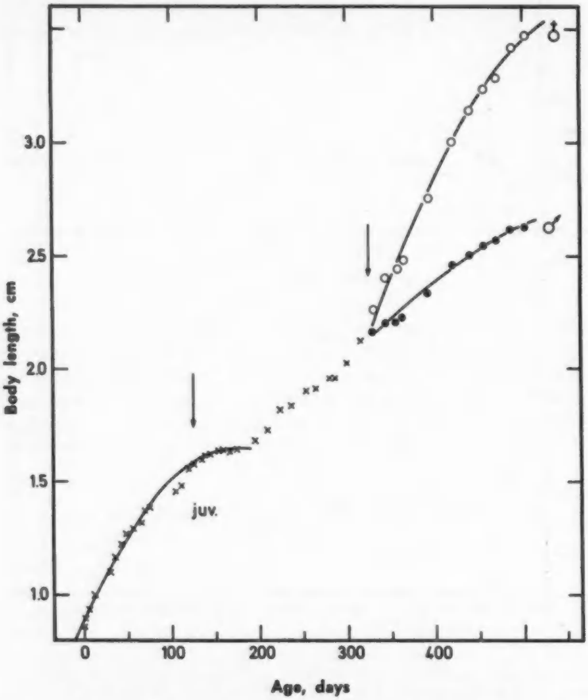
The temperature at which the growth rate is maximal, τ_{mg}, is given implicitly by

$$k_0 p_k \, e^{p_k \tau_{mg}} \, w^{n-m} = \frac{p_2 \, b \, e^{-p_2 \tau_{mg}} - p_0 \, a \, e^{p_0 \tau_{mg}}}{(b \, e^{-p_2 \tau_{mg}} + a \, e^{p_0 \tau_{mg}})^2} \qquad \ldots\ldots(C12)$$

which must be solved by iteration. The broken line in App. Fig. 19 indicates such solutions for males. Plotting τ_{mg} against weight for juveniles, females, and males describes the temperature trends ensuring maximum growth rate during the whole life of the fish (App. Fig. 20). The end point of each curve is $W_{\infty m}$, by definition. The apparent discrepancy between males and females is due to the choice of independent variable. If it is assumed that the two sexes grow towards $W_{\infty m}$ at the same relative rate of speed, i.e. if temperature is plotted against

$$\frac{w - W_{mat}}{W_{\infty m} - W_{mat}}$$

where W_{mat} is the weight at maturity, the two curves almost cover each other.



APP. FIG. 18. *Lebistes*. Length plotted against age for a batch of fish kept at low temperatures (17–19 C), with eye-fitted growth curves. Arrows indicate the times when the first and the last specimen could be identified to sex. The juveniles seem to approach an asymptotic size of their own before becoming mature. App. XIII.

It should be interesting to know if the fish "prefer" the temperature at which they grow fastest. If they do, the two sexes stick together whereas the new-born young ones move away from them towards a higher temperature, thus escaping predation by adults.

EXAMPLE 13. GILL AND BODY SURFACE AREAS AND METABOLIC RATE

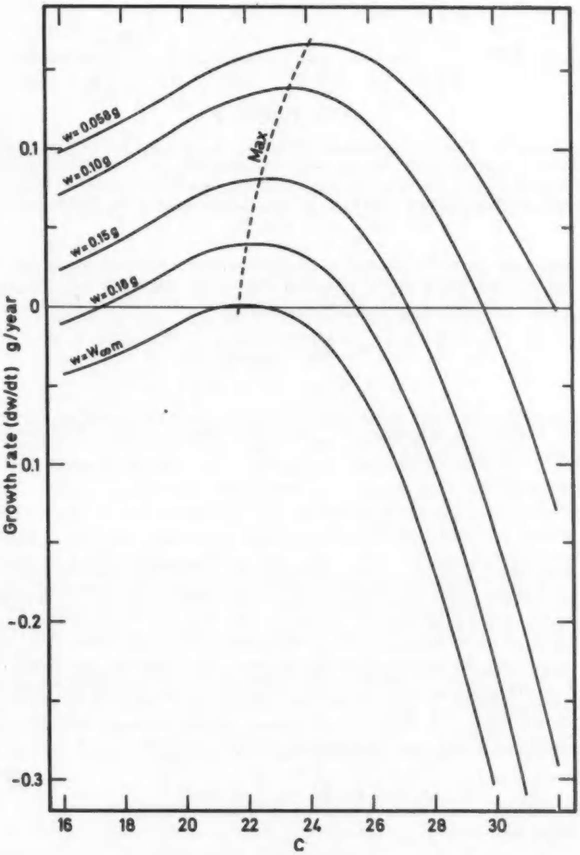
ESTIMATES OF n, n_g, A_b AND A_g

The parameters of respiratory surface and of oxygen consumption in relation to surface are given by

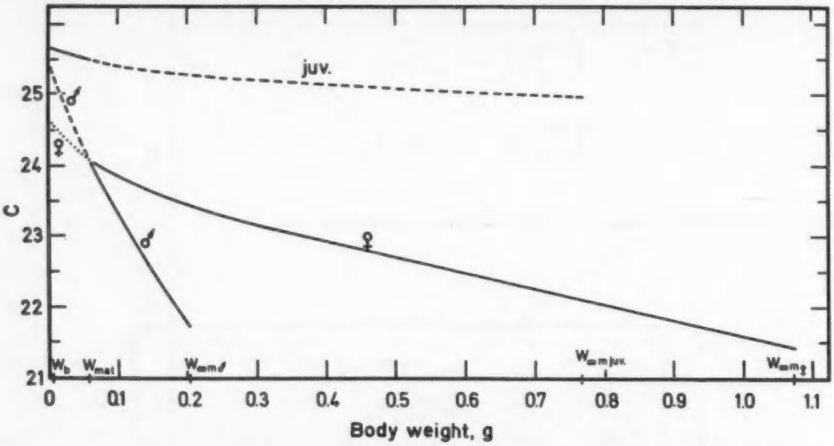
$$\left.\begin{aligned} S_b &= A_b\, w^{2/3} \\ S_g &= A_g\, w^{n_g} \end{aligned}\right\} \quad \ldots.(A6)$$

$$\left.\begin{aligned} \left(\frac{dO_2}{dt}\right)_b &= -\,B_b\,S_b \\ \left(\frac{dO_2}{dt}\right)_g &= -\,B_g\,S_g \end{aligned}\right\} \quad \ldots\ldots(A7)$$

where the subscripts *b* and *g* stand for body and gills respectively.



App. Fig. 19. *Lebistes*. Growth rates of males of various sizes over a range of temperatures. The broken line connects the maxima. App. XIII.



APP. FIG. 20. *Lebistes*. The temperatures producing maximum growth, plotted as a function of body weight. W_b: weight at birth; W_{mat}: weight at maturity; $W_{\infty m}$: highest asymptotic weights (the maxima in App. Fig. 17). Parts of the curves which cannot be made the object of observation (immature fish of adult size; mature fish of juvenile size) are dotted. App. XIII.

The parameters are generally difficult to estimate and the relevant literature correspondingly scarce and not too reliable. Price (1931, cited by Fry 1957) measured the gill area of the small-mouthed black bass (*Micropterus dolomieu*) and found

$$n_g = 0.785; \quad A_g = 8.65 \ \mathrm{cm^2 g^{-0.785}}$$

so that

$$0.667 < n < 0.785$$

Gray (1954) studied the gill area of 31 species of marine fishes. Disregarding interspecific differences equation A6, rearranged as

$$\frac{S_g}{w} = A_g \, w^{(n_g - 1)}$$

provides an estimate of n_g. App. Fig. 21 is a log scale plot of gill area per unit body weight against body weight (from Gray's Table I). There is one entry for each species. Six species are described by Gray as active and rapidly swimming (circles in App. Fig. 21). Four others are called sluggish. In the latter group (squares in App. Fig. 21) I have included the eels. Obviously, the more active the species (i.e. the higher its maintenance catabolism) the larger its gill area. The regressions are not significant in the small groups of active or sluggish fishes, but for the remaining 19 species of more ordinary behaviour we get

$$S_g/w = 13.92 w^{-0.181} \ \mathrm{cm^2 g^{-1}}$$

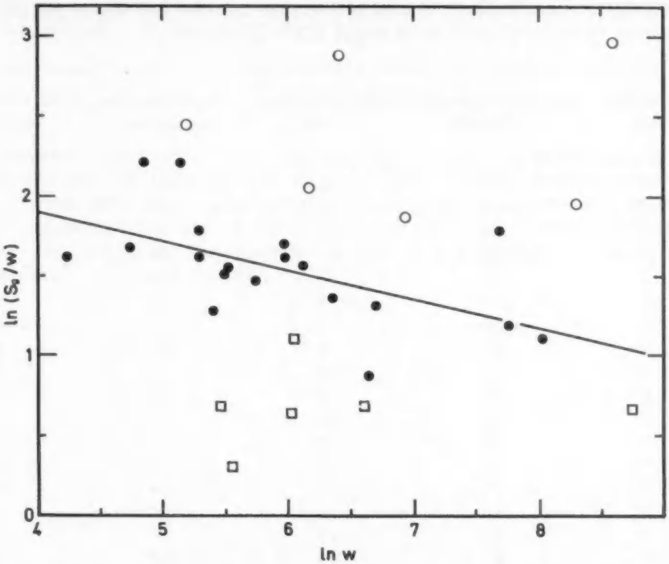
$$n_g = -0.181 + 1 = 0.819$$

95% confidence interval:

$$0.805 < n_g < 0.833$$

from which

$$0.667 < n < 0.833.$$



APP. FIG. 21. Relative gill surface area, S_g/w, as a function of body weight, w. Thirty-one species of marine fishes (from Gray). Circles indicate particularly active species, squares particularly sluggish ones. The regression line is a least squares fit to the observations, omitting circles and squares. App. XIV.

It is doubtful, however, whether the assumption holds, that n_g is the same in all species. The body surface area of fishes varies appreciably as a result of differences in shape (Gray, 1953) and as a result of different development of fins and other protuberances. If skin respiration is at all significant, its importance varies with the ratio between gill and body areas. For constant n_g, n varies, and vice versa. To determine n_g in a fish with a small gill area and a large body area Mr S. Wiedemann Smith has made some pilot observations on *Zoarces viviparus*, a slender and sluggish fish likely to fulfil the requirements. On the second left gill bar the number of filaments was counted, and so was the number of lamellae on one of the longer filaments. The breadth and height of a lamella was measured. Assuming the lamellae to be infinitely thin rectangular plates an index of gill area is: breadth of lamella × height of lamella × number of lamellae on filament × number of filaments.

With isometric growth the two measurements should be proportional with body length whereas the numbers should be independent of body size. This would make gill surface proportional with l^2, as required. The observations are listed in App. Table X. A log scale linear regression of each quantity against 1 provided the following estimates of the powers of length with which they are proportional:

	Power, with 95% confidence interval	Isometric value of power
Breadth of lamella	0.948 ± 0.122	1
Height of lamella	0.931 ± 0.165	1
Number of lamellae	0.902 ± 0.131	0
Number of filaments	0.156 ± 0.061	0
Sum of powers	2.937	2

APP. TABLE X. *Zoarces viviparus*. Counts and measurements for estimate of gill surface index (App. XIV).

Length of fish (cm)	Breadth of lamella (10^{-3} cm)	Height of lamella (10^{-3} cm)	No. of lamellae on filament	No. of filaments on gill bar
7.5	25	9	35	45
7.5	28	8	40	47
10.0	38	11	47	46
11.0	41		40	46
11.5	44	15	54	45
12.0	41	14	54	51
12.5	38	12	55	48
13.0	50	12	60	46
14.0	44	11	70	48
15.0	50	15	65	48
15.5	50	16	66	
17.0	59	16	73	51
19.5	72	21	87	54
19.5	75	19	76	50
22.5	62	24	93	53
23.0	84	25	97	52
23.5	81	24	115	57

The isometric values for lamellar growth are within the confidence intervals of the estimates. The numbers, however, increase disproportionately, particularly the number of lamellae per filament which increases almost proportionately with body length. The effect is that, in *Zoarces viviparus*, gill area is proportional with body weight, or almost so. This was to be expected if n, rather than n_g, is a constant for fishes. However, there is no theoretical background for expecting n constant, but empirically, there is a good deal of evidence (see the foregoing Appendixes) that putting $n = 5/6$ is not far off the mark.

When fishes of the same size are compared, it is found (Gray, 1954) that the ratio gill area/body area is 5 or 10 times higher in active fishes than in sluggish ones. For medium-sized fishes it is of size order 10 in active species and 1 in sluggish ones. Skin respiration, therefore, is probably of little importance in active fishes, except in the youngest stages, whereas in sluggish fishes it may or may not be important, depending on the actual rate of oxygen consumption of fish skin. Facts on this subject are scarce. I have found one paper only (Krogh, 1904) dealing with the partitioning of total respiration between gill and skin respiration.

Krogh (1904), using European eels, *Anguilla anguilla*, in spite of obvious technical difficulties, managed to obtain data which are at least suggestive. The method was to carry out two sets of experiments using the same eels in both. In one set, the animals were left free and undisturbed, in another the mouth and gill slits were closed by sutures. Clearly, only a fish with a low metabolic rate would stand a treatment like that and in fact the eels were often moribund at the end of the second experiment. The mean values from sets VI, VII, and VIII are: w = 118 g, τ = 16 C, total oxygen consumption = 33.90 cm^3 kg^{-1} hours^{-1}, oxygen consumption through the skin = 21.36 cm^3 kg^{-1} hours^{-1}, ratio skin respiration/total = 0.63. To evaluate these data the body and gill areas must be known. Krogh measured the surface (including fins but omitting the buccal cavity) of an eel 70.0 cm long and weighing 680 g. He found S_b = 916 cm^2. Hence, $A^b = S_b/w^{2/3}$ = 11.8 cm^2 g$^{-2/3}$. The gill area was not measured, but from Gray (1954) can be borrowed data on the American relative of the European eel, *Anguilla rostrata*. Gray found, for

$w = 428$ g, $S_g = 1293$ cm^2. Putting $n_g = 1$, as found above for *Zoarces*, another slender and sluggish fish, gives $A_g = S_g/w = 3.02$ cm^2 g^{-1}. For an eel of 118 g the above parameter estimates give

$$S_g = 356 \text{ cm}^2;\ S_b = 285 \text{ cm}^2;\ S_b/(S_g + S_b) = 0.44.$$

According to this, the body area is less than half the total area and the skin respiration is more than half the total respiration, i.e. $B_b > B_g$. This is scarcely feasible. Remembering the difficulties encountered when measuring surfaces and oxygen consumption, a reasonably conservative judgment is that, in the eel, body and gills contribute each to about half the total surface and to half the total oxygen consumption. The value of n, accordingly, will be about midway between 2/3 and 1 ($= n_g$) i.e. $n = 5/6$.

NOTES

Occurrence of Larval Herring (*Clupea pallasii*) in the Strait of Georgia during July 1966

In a general survey of production processes in the Strait of Georgia, several species of larval fish were caught during July 1966 in the surface waters at the southern end of the Strait. Among these were large numbers of larval herring (*Clupea pallasii*) which have not been reported previously as occurring in the open surface waters. In addition, the size composition indicated that an extensive spawning must have occurred at a much later period than spawnings actually observed during the late winter or early spring months of the same year.

During the study reported here, larval herring were caught by a surface trawl towed between two vessels. This trawl was designed to catch adult, juvenile, and larval fish, as well as zooplankton in the same tow. Larval fish and zooplankton were caught separately and undamaged in the 351-μ mesh (measured on the bar) Hensen net secured to a special panel of netting at the aft end of the codend. The standard Hensen plankton net, measured 28.75 inches (73 cm) in diameter at the mouth. Although the 2-inch (5-cm) and 1-inch (2.5-cm) mesh in the body of the trawl net may have deflected some larvae into the codend, however, for an estimate of abundance it was assumed that the mouth of the 0.5-inch (1.3-cm) mesh codend, in front of the Hensen net, influenced the capture of larval herring, so that the cross-sectional area of the water cylinder swept by the net was taken to be 24 ft^2 (2.2 m^2).

At each station, the two-boat surface trawl was towed for a period of 10 min and at a speed of 3 knots (5.6 km/hr). The total area surveyed was 450 nautical $miles^2$ (1550 km^2), and the number of herring larvae caught in 25 tows was 2824. Thus with these data the total estimated number of larval herring was 2×10^8, to a depth of 2.4 m. This may be considered as a minimum number because of the efficiency of the fishing gear, the conservative allowance for the effective mouth opening, and the fact that a stratum only 8 ft (2.4 m) deep is considered, whereas in other parts of the Strait larval herring have been found down to 15 fath (30 m) during daylight hours (Mr J. Rees, personal communication). Average survival of herrings eggs to the larval stages collected here is probably less than 0.1% (Stevenson, 1962, p. 772; Taylor, 1964, p. 6). Hence, the number of eggs spawned was likely of the order of 2×10^{11} to 2×10^{12}, which represents 2×10^7 to 2×10^8 adult herring, or 2000–20,000 tons.

The actual location of stations and the number and size frequency of larval herring caught are shown in Fig. 1 and Table I. The data reported in Table I are from 25 out of 29 daylight tows in which herring larvae were caught.

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

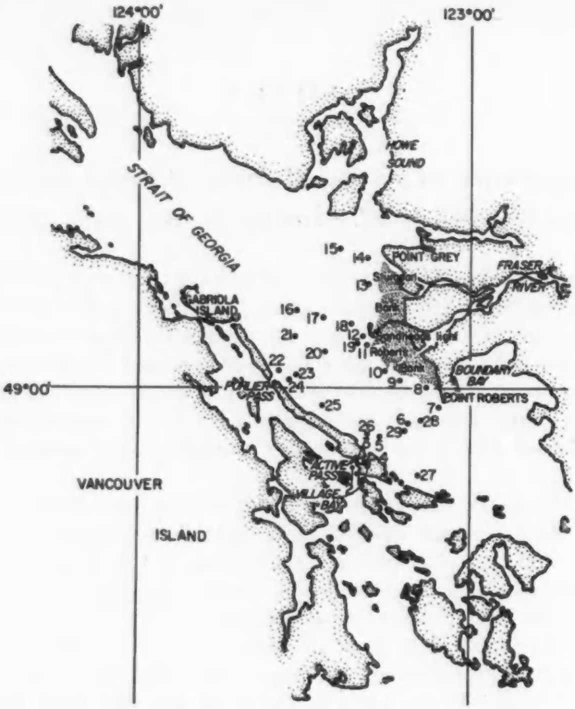

124°00'
123°00'
HOWE SOUND
STRAIT OF GEORGIA
15
14
POINT GREY
FRASER RIVER
13
Sturgeon
Bank
GABRIOLA ISLAND
16
17
18
12
Sandheads light
21
20
19
11
Roberts
Bank
22
23
10
BOUNDARY BAY
49°00'
PORLIER PASS
24
9
8
POINT ROBERTS
25
7
6
28
26
29
5
ACTIVE PASS
4
27
VILLAGE BAY
VANCOUVER
ISLAND

FIG. 1. Location of the stations, numbered in sequence, where tows were made with a two-boat surface trawl July 4–8, 1966.

No larval herring were caught in four tows taken through Active Pass. All other stations at which herring larvae were caught were in the area of the southern Strait of Georgia, between the Fraser River delta and Vancouver Island, with largest numbers generally close to the Fraser River estuary.

Knowing the average length of larval herring and such factors as the time required for the eggs to hatch, the length of larvae when they hatch, and the growth rate, it is possible to estimate the approximate time when spawning occurred. Thus it takes about 2 weeks for the larvae to hatch in the warmer waters near the end of the spawning season and the larvae hatch at a length between 6–8 mm. Larvae hatched out early in the season grow only about 0.3 mm per day and those hatched in early May have been shown to grow 0.8 mm per day (Stevenson, 1962). Since the average length of 713 larvae caught between July 5–8, 1966 was 24 mm, spawning probably occurred 5–6 weeks prior to the date of capture, i.e. May 22–June 4, 1966. The wide spread in the length of larvae reported in Table I suggests that several spawnings occurred, some as early as May 15–21, and some as late as June 5–11,

TABLE I. Number and percentage length-frequencies of larval herring caught in the two-boat surface trawl from Strait of Georgia, July 5–8, 1966. Times PDST (+7 Time Zone).

Station No.:	5	6	7	8	9	10	11	12	13	14	15	16	17
Time/day:	0609 0619/5	0753 0803/5	0837 0847/5	0926 0936/5	1021 1031/5	1100 1110/5	1213 1223/5	1300 1310/5	1350 1400/5	1440 1450/5	1504 1514/6	0849 0859/7	0927 0937/7
Depth to sea bottom (*fath*):	85	68	66	35	49	54	60	58	52	24–43	132	190	142
Fork length (*mm*)													
13													
14					2								
15					2								
16						2							
17						4							
18			3		8	6							
19			12	4	4	4							
20	20		24	8	4	2					7	7	4
21	20		28	20	10	12					3		
22	60		21	40	18	16	8				10	7	4
23			12	24	18	22	17				10	20	12
24				4	14	12	8	4	4		20	26	20
25					8	6	8	14	4		20	33	24
26					6	6	8	22	8		20	7	16
27							17	32	20	4	7		12
28					2			14	36	12			4
29								4	16	24	3		4
30					2	4	17	4	4	40			
31					2	4	17	4	8	16			
32													
33								2		4			
34													
35													
Avg length (*mm*)	21.4	–	20.9	21.8	22.5	22.7	26.6	27.7	27.8	29.7	24.3	23.9	24.9
No. measured	5	–	33	25	50	50	12	50	25	25	30	15	25
No. in sample	5	117+	133	271	500+	350+	12	108	30	95	61	35	33

(*Continued*)

TABLE I. Number and percentage length-frequencies of larval herring caught in the two-boat surface trawl from Strait of Georgia, July 5–8, 1966. Times PDST (+7 Time Zone). — (*Concluded*)

Station No.:	18	19	20	21	22	23	24	25	26	27	28	29
Time/day:	1007 1017/7	1057 1107/7	1145 1155/7	1240 1250/7	1401 1411/7	1510 1520/7	1541 1551/7	1634 1805/7	1755 0645/8	0635 0753/8	0734 0817/8	0807 0817/8
Depth to sea bottom (*fath*):	84	82	142	182	62	96	75	80	82	76	62	78
Fork length (*mm*)												
13							5					
14												
15												
16								4				
17									2		3	
18						10		2	2		7	12
19		2		2				2	2		17	14
20		2	12	8	17			6	4		23	10
21		12	4	2		10		6	8		23	14
22	4	6		2	17	20		8	4		17	18
23	4			12	32	20	5	14	16	50	7	20
24	8	8	8	28	17	20	15	16	26	50	3	8
25	32	22	16	26		10	40	16	20			2
26	20	22	20	14		10	25	16	12			2
27	16	18	12	6	17		5	10	4			
28	4	2	8									
29	8	4	16									
30	4	2	2									
31												
32												
33												
34												
35							5					
Avg length (*mm*)	25.9	23.5	25.7	24.1	23.2	22.8	25.0	23.5	23.6	22.5	20.5	21.3
No. measured	25	50	25	50	6	10	20	50	50	2	30	50
No. in sample	135	93	34	98	6	12	28	264	156	2	54	192

Avg length 713 larvae = 24 mm
Total measured = 713
Total in sample = 2824

1966. All of these estimated spawning periods are considerably later than any reported previously (Taylor, 1964, p. 3; Outram, 1967).

It is only possible to speculate where this spawning may have occurred. Of all the known spawning areas in the southern Strait of Georgia, the most probable area would be in Boundary Bay, where extensive beds of eelgrass (*Zostera marina*) in the upper and lower intertidal zone are known to exist. Eelgrass is one of the major substrates used by spawning herring in the Strait of Georgia (Outram, 1957). With increasing amounts of sunlight in the late spring, the more rapid growth of aquatic flora in subtidal or deeper waters may enable herring to spawn on eelgrass in localities where observations of spawn deposition from vessels or on shore are not possible.

The location of spawn deposition, of course, is the first factor in determining the distribution of herring larvae. Time of spawning, amount of deposition, and type of substrate are important factors prior to the time of hatching, but the planktonic behavior of herring larvae prior to "metamorphosis" is a factor of prime importance. At their planktonic stage, herring larvae exhibit more or less passive movements, and are therefore at the mercy of both water currents and factors affecting water movement such as winds.

In the southeastern region of the Strait of Georgia, Waldichuk (1957, Fig. 55) shows that the prevailing surface wind during the spring transition, April–May, and summer, June–September, is in a southeast direction. The effect of the southeast surface wind and the counterclockwise gyral that is presumed to exist in the surface circulation of the southern Strait of Georgia (Waldichuck, 1957, p. 418) suggests that larvae hatched from a spawn deposition near Boundary Bay or along the southeast shore of the Strait of Georgia, would be transported around Point Roberts and along Roberts Bank and Sturgeon Bank off the mouth of the Fraser River.

The number of larval herring caught in the surface tows indicates that their distribution pattern throughout the southern Strait of Georgia is further influenced by the tidal cycle and the persistent seaward movement of freshwater from the Fraser River (Tully and Dodimead, 1957). This two-fluid system, in which a surface layer of fresh- or brackish water moves over a body of seawater, creates a condition of highly stratified waters in this region of the Strait. It is in such an environment of relatively low salinity that young herring after "metamorphosis" are known to concentrate (Hourston, 1959). The process of metamorphosis, whereby larvae cease to exist as free floating organisms, occurs at a length of about 26 mm for Pacific herring in British Columbia waters (Stevenson, 1962). At this stage, all the fins have been developed and the postlarval herring become more independant of water movement.

The average length of larval herring caught off the Sturgeon Bank (Tows No. 11–14, 18) was slightly longer than of those caught in all other tows in the southern Strait of Georgia. These herring had grown to the stage where metamorphoses of postlarval herring starts. Thus they had hatched earlier than larvae caught in other surface tows and remained within the influence of the counterclockwise gyral for a longer period, at the same time reaching a greater distance from their spawning grounds.

Fisheries Research Board of Canada W. E. Barraclough
Pacific Oceanographic Group, Nanaimo, B.C.

Received for publication May 18, 1967.

REFERENCES

Hourston, A. S. 1959. Effects of some aspects of environment on the distribution of juvenile herring in Barkley Sound. J. Fish. Res. Bd. Canada, **16**(3): 283–308.

Outram, D. N. 1957. Guide to marine vegetation encountered during herring spawn surveys in southern British Columbia. Fish. Res. Bd. Canada, Biol. Sta., Nanaimo, B.C., Circ. No. 44. 18 p.
1967. Herring spawn abundance in British Columbia, 1966. Ibid., Circ. No. 77. 17 p.

Stevenson, J. C. 1962. Distribution and survival of herring larvae (*Clupea pallasi* Valenciennes) in British Columbia waters. J. Fish. Res. Bd. Canada, **19**(5): 735–810.

Taylor, F. H. C. 1964. Life history and present status of British Columbia herring stocks. Bull. Fish. Res. Bd. Canada, No. 143. 81 p.

Tully, John P., and Allan J. Dodimead. 1957. Properties of the water in the Strait of Georgia, British Columbia, and influencing factors. J. Fish. Res. Bd. Canada, **14**(3): 241–319.

Waldichuk, Michael. 1957. Physical oceanography of the Strait of Georgia, British Columbia. Ibid., **14**(3): 321–486.

A New Plastic-Bag Water Sampler

The plastic-bag sampler described in this note was developed in connection with studies of diel cycles and seasonal variations in the populations of the plankton communities of some mountain lakes in Banff and Jasper National Parks. Most of these lakes are 2 km or more from the nearest road, small (2–25 ha), and range from 10 to 30 m in depth. The plankton communities of the lakes are mainly comprised of small forms: rotifers, small crustaceans (0.5–1.5 mm), larger diaptomid copepods and daphnids (2–3 mm), and small phytoplankters, 90–100% of which may be nannoplankton. No larger, fast-swimming crustaceans have been found in these lakes. Sampling is usually carried out from an inflatable dingy or raft which, considered with the lake features already noted, precludes the use of metering nets or other elaborate equipment for large volume sampling at any given depth.

Scale-drawings of the plastic-bag sampler are given in Fig. 1. The end pieces, carriage block, housing for pulley and spring, and the closing plate are made of aluminum, and the swivels, suspension chains, pulley, carriage catch, and carriage ring are brass. The base plate is machined from lucite, and the closing plate is faced with soft, neoprene rubber of the type used in skin divers' wet suits. The two rods on which the carriage slides, the supporting spindles for the base and closing plates, and the release mechanism are made of stainless steel rod and thin plate. The release mechanism is designed to fold over to either side to facilitate storage. The carriage rods and plate spindles are secured in holes in the aluminum end pieces with set screws so that adjustments in the carriage travelling distance and in the positioning of base and closing plates are easily made. The prototype was fitted with a strong clock spring, but a heavy-duty stainless spring would be preferable.

The sampler chamber is a 1-mil plastic freezer bag 4 × 8 × 18 inches (10 × 20 × 46 cm). The bag is applied to the sampler by removing the base plate, putting the base-plate spindle and drain tubing through holes in the bag bottom from inside the bag, and fastening the bag to the base plate with a heavy, rubber ring. After the base plate is replaced in the end piece, the top of the bag is pulled over the carriage ring from inside the ring. The carriage ring is then closed against the closing plate and a rubber ring (previously placed over the closing plate) is pulled over the closing plate onto the carriage ring to secure the plastic bag to the ring. A groove in the carriage ring keeps this rubber ring in place. Because no metal parts are exposed to the water sample, the sample is suitable for chemical analysis and for primary production experiments.

Figure 2 illustrates the cocking process. With one hand, the carriage apparatus is drawn back about ⅔ of the distance from the closing plate while, with the other hand, the loose plastic bag is drawn back around the base plate. The carriage apparatus is then drawn back until the steel pin on the carriage

J. Fish. Res. Bd. Canada, 24(11), 1967.
Printed in Canada.

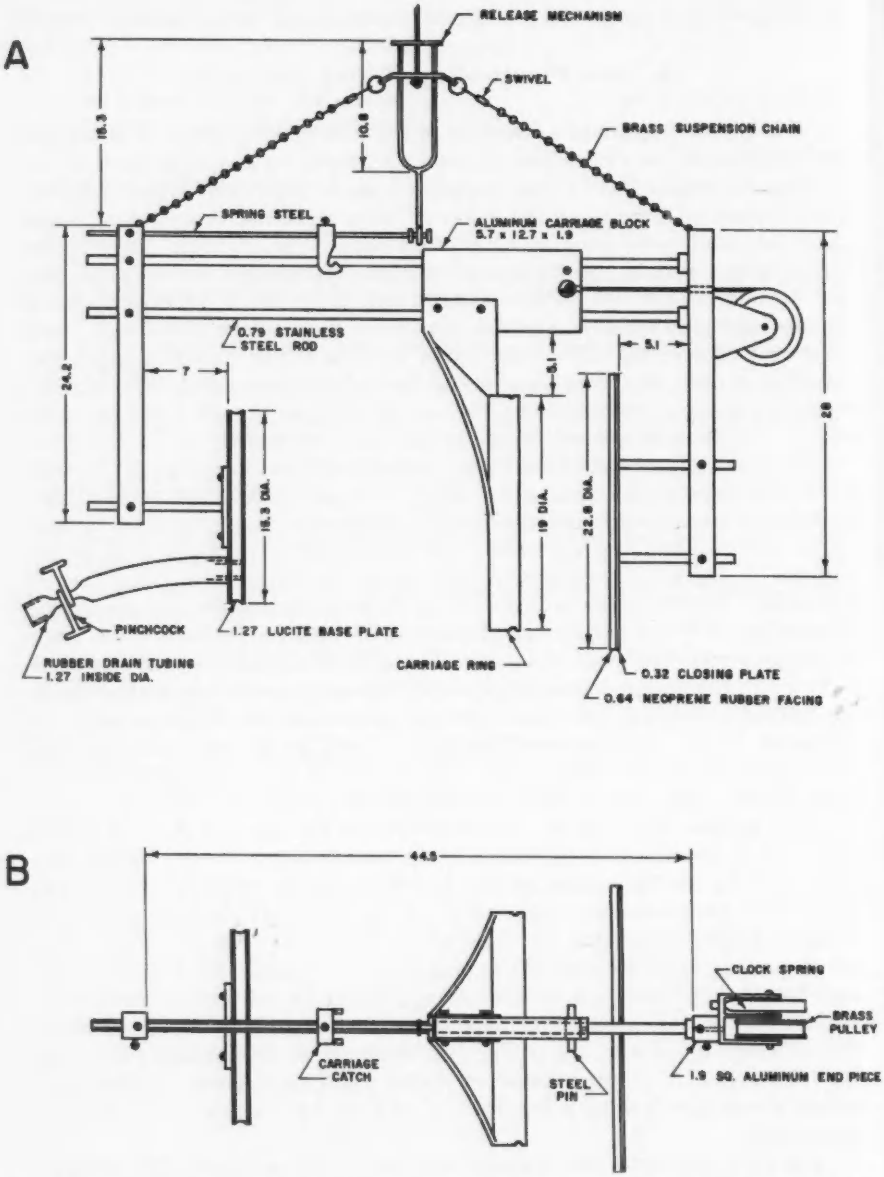
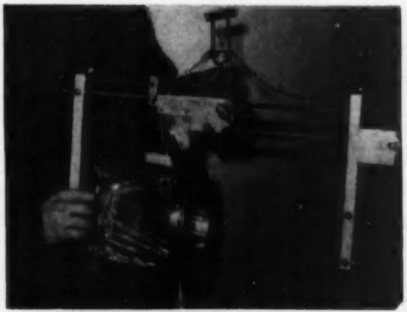

A
RELEASE MECHANISM
SWIVEL
BRASS SUSPENSION CHAIN
15.3
10.8
SPRING STEEL
ALUMINUM CARRIAGE BLOCK
5.7 x 12.7 x 1.9
0.79 STAINLESS
STEEL ROD
24.2
7
5.1
5.1
28
15.3 DIA.
19 DIA.
22.8 DIA.
PINCHCOCK
1.27 LUCITE BASE PLATE
RUBBER DRAIN TUBING
1.27 INSIDE DIA.
CARRIAGE RING
0.32 CLOSING PLATE
0.64 NEOPRENE RUBBER FACING
B
44.5
CLOCK SPRING
BRASS
PULLEY
CARRIAGE
CATCH
STEEL
PIN
1.9 SQ. ALUMINUM END PIECE

FIG. 1. Scale drawings of the plastic-bag sampler (dimensions in centimetres). A, elevation, in partly closed position, without the plastic bag. B, top view, without release mechanism, suspension chains, and drain tube.



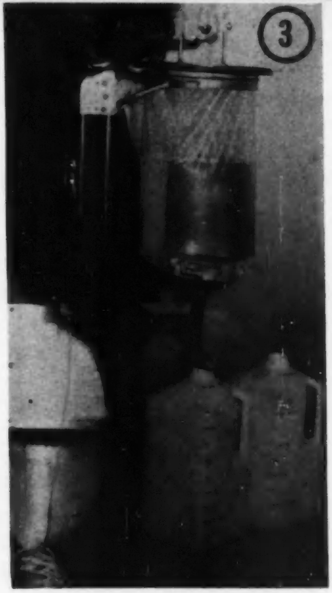


FIG. 2. Cocking the plastic-bag sampler.
FIG. 3. Draining the sample into calibrated containers.

block engages the carriage catch (see Fig. 1B). The bag is kept taut over the base plate during this final cocking process, and the bag bulk is then tucked between the base plate and the carriage ring. If care is exercised in cocking the apparatus, a reasonably consistent sample size of about 8 litres is obtained.

The sampler is triggered by sending a messenger down the suspension line. This depresses the spring-steel rod and carriage catch, allowing the carriage apparatus to be pulled from the base plate to the closing plate by the spring-loaded pulley. The sample is released in the manner shown in Fig. 3.

The sampler design permits reasonably accurate sampling of surface layers and water layers near lake bottoms. Because of the horizontal action of the sampler, the samples should be more representative of discrete water layers than those from samplers featuring vertical cylinders. The small surface area presented to the water (see Fig. 1B) and small overall bulk appear to reduce the amount of water and plankton carried from one depth to another, to reduce turbulence, and to minimize possible zooplankton avoidance reactions due to large visible bulk. Little disturbance is created in the water by the closing mechanism because so little displacement is involved when the water sample is enclosed by the carriage ring and plastic bag. The features are in accordance with the conclusions of Fleminger and Clutter (1965) that both visual and mechanical disturbances can be involved in avoidance reactions.

A number of comparative samples were taken in March 1967, using the plastic-bag sampler and a Wisconsin-type plankton net of #20 bolting silk (mouth area 450 cm^2) towed vertically at 0.5 m/sec (Rawson, 1942). Sampling was done through an ice hole in Herbert Lake, near Lake Louise in Banff National Park. Air temperatures varied from −1 C to +3 C, and water temperatures ranged from 0 C at the surface to 4.3 C near bottom. There was no wind. Two nets were used, and precautions were taken to keep them from freezing.

The average numbers of copepods (*Diaptomus sicilis*) per litre for 10 depths, calculated from five sampling runs with the plastic-bag sampler, were:

Depth (*m*):	1	2	3	4	5	6	7	8	9	10
Avg no. of copepods per litre:	2.0	9.1	9.1	6.6	4.1	4.1	4.6	5.2	5.2	5.6

When the net samples, based on the theoretical maxima of water strained (Fleminger and Clutter, 1965), were compared with the samples taken with the plastic-bag sampler (see Table I) the net efficiency was found to vary from 13.9% for a 5-m tow to 25.8% for a 10-m tow. These figures compare closely with the 20–25% found by Rawson (1942) for the same type of net, towed at the same rate, in comparison with a 20-litre plankton trap (type not noted).

TABLE I. Calculated net efficiencies in comparison with the plastic-bag sampler.

Depth of vertical net tow (*m*)	No. of single tows	No. of copepods/tow (*avg*)	Range	Calculated net efficiency (%)
5	3	180	169–196	13.9
7.2	2	372	363–381	20.4
10.5	4	680	627–712	25.8

These preliminary tests indicate that the plastic-bag sampler is capable of giving a good estimate of the population density of small, limnetic zooplankters. Further tests of efficiency and comparisons with other types of traps will be conducted.

This work was done in conjunction with the limnological research program of the Canadian Wildlife Service. Thanks are due to Jim Lisoway, National and Historic Parks Branch, who drew the plans.

Canadian Wildlife Service
c/o Biology Department
University of Calgary, Calgary, Alta.

R. STEWART ANDERSON

Received for publication April 4, 1967.

REFERENCES

FLEMINGER, ABRAHAM, AND ROBERT I. CLUTTER. 1965. Avoidance of towed nets by zooplankton. Limnol. Oceanog., **10**(1): 96–104.

RAWSON, DONALD S. 1942. A comparison of some large alpine lakes in western Canada. Ecology, **23**(2): 143–161.

Measuring Organic Matter Retained by Aquatic Invertebrates[1]

Assimilation (absorption of food from the gut lumen) by aquatic invertebrates has been measured as organic matter ingested minus organic matter in feces by several authors (Corner, 1961; Conover, 1962, 1964; Johannes and Satomi, 1966). Two assumptions implicit in this calculation deserve critical comment.

The first assumption is that feces contain organic matter derived *entirely* from food. Actually, feces also contain organic matter derived from assimilated materials, such as mucous and chitinous intestinal secretions (e.g. Forster, 1953; Gauld, 1957; Reeve, 1963).

The second assumption is that *all* unassimilated food is released in feces. The probability that some of this organic residue is released in solution is not taken into account. Johannes (1964) reported that the release of dissolved organic phosphorus by a marine amphipod decreased rapidly as its gut emptied of food. R. E. Johannes et al. (unpublished results) have found that release of dissolved free amino acids by the flatworm, *Dugesia dortocephala*, decreases by more than two orders of magnitude during starvation, whereas its respiration rate decreases by only about 50%. Both observations suggest that dissolved organic release products may be derived in part from undigested food. Furthermore, Conover (1966) has pointed out that soluble organic materials in food may be lost directly to the water as a result of mechanical damage to the food during its seizure and manipulation by the feeding organism.

The first assumption thus leads to an underestimation of assimilation; the second leads to an overestimation. Because the magnitude of these two errors is unknown, we cannot even determine whether assimilation efficiencies calculated in this manner are too low or too high.

Other workers have estimated assimilation by measuring the amount of C14-labelled food incorporated into the tissues of feeding animals (e.g. Sorokin, 1966). This technique is also unsatisfactory owing to the exchange of labelled food compounds in the gut lumen with unlabelled compounds in the gut wall. As Christensen (1962) states, "If a chemical structure mediates transport across a membrane, it can obviously work in both directions, and much of the flux in one direction will be cancelled out by flux in another, so that net flux may be only a small fraction of the total flux." Measurement of absorption of labelled food from the gut thus yields an overestimate of net food absorption (e.g. see Jacobs, 1965) and is therefore of questionable value in studies of energy flow. Techniques used to correct such assimilation estimates for this exchange diffusion would be extremely difficult to apply to small aquatic animals.

---

[1] Contribution No. 140 from the University of Georgia, Marine Institute, Athens, Ga.

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

We thus seem forced either to define assimilation to fit whatever method of measurement we use (and acknowledge that we are not really measuring absorption of food from the gut, but making an approximation of unknown accuracy) or substitute some alternative concept of food utilization more amenable to accurate measurement. In this report we have determined a useful, and we believe, operationally sounder parameter of energy metabolism by simply subtracting the total rate of release of particulate and dissolved organic carbon by an aquatic invertebrate from the rate of input of organic carbon in the food.

This is a measure of what might be called retention of organic carbon; that is, the rate at which ingested organic carbon is retained by the animal for growth and respiration. Measurement of this rate requires no knowledge of what fraction of the release products is undigested food and what fraction is derived from assimilated material. Regardless of the origin of organic release products, they represent a loss to the animal. It is this total loss subtracted from the food input, which constitutes the real measure of the organic carbon available to the animal for growth and respiration.

Although we calculate the rate of retention of organic carbon as (organic carbon ingestion rate − total organic carbon release rate), it can be seen that this value is also equal to (organic carbon assimilation rate − release rate of assimilated organic carbon). That is, if;

$$A = I - U$$

and

$$X = I - U - E$$

then

$$X = A - E$$

where A = organic carbon assimilation rate; I = organic carbon ingestion rate; U = rate of release of unassimilated organic carbon; X = rate of retention of organic carbon; E = rate of release of assimilated organic carbon. Thus, retention will always be less than assimilation.

Here, as an example of the application of this method, we report the determination of retention of organic carbon by the benthic estuarine decapod, *Palaemonetes pugio*, feeding on the diatom, *Nitszchia closterium*. Adult *P. pugio* 22–25 mm long from eye to tip of telson were collected from tidal creeks at Sapelo Island, Georgia. The mean fresh and dry weights of 50 animals in this size range were 160 and 50 mg, respectively. Unialgal cultures of *N. closterium* were cultured in 12-inch diam glass-covered finger bowls in seawater enriched with modified Miquel's solution (Allen, 1914). The cultures were grown at 26 ± 1 C in a chamber illuminated with white fluorescent lamps. Cultures were used in feeding experiments while still in the logarithmic growth phase 6 days after inoculation.

In order to measure ingestion and egestion rates, we divided *N. closterium* cultures into two equal portions. Diatoms from one portion were removed, deposited on a tared glass filter, rinsed briefly in distilled water to rinse off adventitious salts, dried at 82 C, and analyzed for organic carbon. Diatoms from the other portion were fed to 15 *P. pugio*. The animals had been fed *N. closterium* for several days beforehand but were deprived of food for several hours prior to the experiments and their guts were empty. The animals were fed ad libitum for 3 hr. During this time and for ½ hr after feeding ceased (the time it took animals to clear their guts), fecal pellets were collected, dried, and subsequently analyzed for organic carbon in order to determine the release rate of particulate organic carbon.

Ingestion rates were determined by subtracting the organic carbon in uneaten food from the organic carbon in the initial food sample. Dissolved organic carbon release rates were determined using *P. pugio* immediately after their removal from the diatom cultures in which they were feeding. They were held for ½ hr in 100 ml filtered seawater, after which the water was filtered through an acid-washed membrane filter (.45 μ pore diam) and the increase in organic carbon in solution was measured. Blanks were run and excretion values were corrected for the dissolved organic carbon which leached from the filters. It is assumed in subsequent calculations that the rates of release of dissolved organic matter measured in this way were characteristic of feeding animals. They may, in fact, be slightly low owing to brief food deprivation during the experiment.

TABLE I. Ingestion, release, and retention of organic carbon for *P. pugio* feeding on *N. closterium*.[a]

	Expt. No.	
	1	2
Ingestion rate (mg organic carbon g dry wt *P. pugio* hr)	1.70	1.60
Fecal release rate (mg organic carbon g dry wt *P. pugio* hr)	.37	.34
Dissolved organic carbon release rate (mg organic carbon g dry wt *P. pugio* hr)	.50	.50
Rate of retention of organic carbon (mg organic carbon g dry wt *P. pugio* hr)	.83	.76
Per cent retention of organic carbon		
$\left(\frac{\begin{bmatrix}\text{Organic carbon}\\ \text{ingested}\end{bmatrix} - \begin{bmatrix}\text{Particulate \& dissolved}\\ \text{Organic carbon released}\end{bmatrix}}{\text{Organic carbon ingested}}\right) \times 100$	49	47

[a]Each experiment is based on measurements made on a group of 15 animals.

Particulate organic carbon was measured as total oxidizable material using the chromic acid digestion method of Fox et al. (1952) as modified by Menzel and Ryther (1964). Samples for dissolved organic carbon analysis were acidified and nitrogen was bubbled through them for 5 min to remove inorganic carbon. Aliquots were then injected into a Beckman carbonaceous analyzer where the organic carbon was rapidly combusted in a stream of oxygen at 950 C and the evolved CO_2 was measured in an infrared CO_2 analyzer.

Roughly one-half the organic carbon ingested, or 0.8 mg per g dry weight of animal per hour, was retained by *P. pugio* for growth and respiration (Table I). In a previous publication (Johannes and Satomi, 1966), we calculated "assimilation" of organic carbon in *N. closterium* by *P. purgio* as 78–79% using the method described in the first paragraph of the present paper. We now believe these values to have little ecological or physiological meaning.

Palaemonetes pugio released dissolved organic carbon almost $\frac{1}{3}$ as fast as they ingested particulate organic carbon and faster than they released organic carbon in feces (Table I). Similar experiments on a variety of other species would be desirable in order to determine whether the high release rate of dissolved organic carbon found here is typical of marine invertebrates. Observations of Webb and Johannes (1967) on release of dissolved amino acids by marine zooplankton support the present finding in suggesting that the release of dissolved organic matter is an important aspect of the energy metabolism of marine invertebrates.

This work was supported by United States National Science Foundation grants and grants from the Sapelo Island Research Foundation. The assistance of P. Lawless and J. Finger and the use of their carbonaceous analyzer is gratefully acknowledged.

Department of Zoology
University of Georgia, Athens, Ga.
R. E. JOHANNES

Laboratory of Phycology
Tokyo University of Fisheries
Konan, Minato-ku, Japan
MASAKO SATOMI

Received for publication February 13, 1967.

REFERENCES

ALLEN, E. J. 1914. On the culture of the planktonic diatom, *Thalassiosira gravida* Cleve, in artificial seawater. J. Marine Biol. Assoc. U.K., **10**: 417–439.

CONOVER, R. J. 1962. Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. Rappt. Procès-Verbaux Réunions, Conseil Perm. Intern. Exploration Mer., **153**: 190–197.

1964. Food relations and nutrition of zooplankton. Narragansett Marine Lab. Occasional Publ., **2**: 81–91.

1966. Feeding on large particles by *Calanus hyperboreus*. *In* Harold Barnes [ed.] Some contemporary studies in marine science. George Allen and Unwin Ltd., London. p. 187–194.

CORNER, E. D. S. 1961. On the nutrition and metabolism of zooplankton. I. Preliminary observations on the feeding of the marine copepod *Calanus helgolandicus* (Claus). J. Marine Biol. Assoc. U.K., **41**: 5–16.

CHRISTENSEN, H. 1962. Biological transport. W. A. Benjamin, Inc., New York. 133 p.

FORSTER, G. R. 1953. Peritrophic membranes in the Caridea (Crustacea, Decapoda). J. Marine Biol. Assoc. U.K., **32**: 315–318.

FOX, D. L., J. D. ISSACS, AND E. F. CORCORAN. 1952. Marine leptotel, its recovery, measurement and distribution. J. Marine Res., **11**: 29–45.

GAULD, D. T. 1957. A peritrophic membrane in calanoid copepods. Nature, **179**: 325–326.

JACOBS, F. A. 1965. Bidirectional flux of amino acids across the intestinal mucosa. Federation Proc., **24**: 946–952.

JOHANNES, R. E. 1964. Uptake and release of phosphorus by a benthic marine amphipod. Limnol. Oceanog., **9**: 235–242.

JOHANNES, R. E., AND M. SATOMI. 1966. Chemical composition and food value of fecal pellets of a marine crustacean. Ibid., **11**: 191–197.

MENZEL, D. W., AND J. H. RYTHER. 1964. The composition of particulate organic matter in the western North Atlantic. Ibid., **9**: 179–186.

REEVE, M. R. 1963. The filter-feeding of *Artemia*. III. Faecal pellets and their associated membranes. J. Exptl. Biol., **40**: 215–221.

SOROKIN, J. I. 1966. Carbon-14 method in the study of the nutrition of aquatic animals. Intern. Rev. Ges. Hydrobiol., **51**: 209–224.

WEBB, K. L., AND R. E. JOHANNES. 1967. Studies of the release of dissolved free amino acids by marine zooplankton. Limnol. Oceanog., **12**: 376–382.

A Simplified Model of a Lake for Instructional Use

The purpose of this note is to describe a model of a lake that can be assembled at a cost of less than $50, with all parts readily available for other use. The only novel aspect of the model is the use of an infrared light bulb as the laboratory equivalent of the sun, a feature so simple and obvious that the lack of its general utilization as a teaching device is astonishing.[1] The influences of sun, wind, and basin configuration can all be studied as independent variables, and a thermal stratification generated within 20–60 min that would otherwise require 20–60 days in nature. Measurements and calculations are entirely comparable to those employed on lakes.

The following materials are required:

(1) *An aquarium*, corresponding to a lake basin. Aquaria 20 × 40 cm in surface area and 25 cm deep have been used, primarily to accommodate standard laboratory thermometers 30 cm in length. Smaller aquaria could be used with a saving in both cost and time required for experimentation.

(2) *A block of polyurethane foam padding 10 cm thick*. This is cut with a hot knife from a larger block to horizontal dimensions approximately 3 cm greater on each side than those of the aquarium, providing an artificial bottom that can be positioned at any desired depth after expulsion of entrapped air bubbles. Other blocks with the upper surface modified to form sills, depressions, and troughs make useful accessories.

The same material in 5 cm thickness can be used to insulate the sides and bottom of the aquaria, leaving a removable strip at the front to permit reading of the thermometers. (It is desirable to restrict the heat exchange between the model and its surroundings since the experiments are designed for use with cold water in a heated room.)

(3) *An electric air gun* or small portable fan as a wind generator. The best position of the wind source depends on the apparatus used and the desired limnological result. A cardboard strip projecting 2 cm above the windward end of the aquarium improves the overall pattern of circulation with the wind entering parallel to the long axis of the aquarium at an angle of about 30° to the horizontal. The wind is best centered on the long axis of the aquarium, but can also be directed to one side.

(4) *Twelve laboratory thermometers* graduated in degrees Centigrade and strapped by elastics to two plastic rulers or wooden strips at 2-cm depth intervals. Notches are cut to hold the thermometers horizontally in place, suspending the set behind the front face of the aquarium.

(5) *Two water-soluble dyes*. One of these must have the property of almost completely dissolving in the uppermost 2 cm of a water column when

---

[1] Dr Joseph Shapiro (unpublished information) developed a similar though less-refined system when he was teaching at Johns Hopkins University some years ago, and this has doubtless happened elsewhere.

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

sprinkled lightly and evenly over the surface as a fine powder. Methylene blue, catechol violet, and several other dyes have been used for this purpose.[2]

Four experiments are described below for general class use, with students working in pairs.

Experiment I. Thermal characteristics and internal seiches in a model of a north temperate lake.— The aquarium is filled to within 1 cm of the top with a mixture of ice and tap water so as to bring the temperature to 4 C throughout. (Winter temperature inversion can easily be demonstrated when ice is present, although some degree of mechanical mixing or wind motion is necessary.) After the removal of excess ice, the lamps are turned on without wind in order to illustrate the infrared absorption characteristics of water. Typical results are shown in Fig. 1 for an uninsulated aquarium using a single 250-w bulb located 20 cm above the water surface. The student is asked to explain the quasi-logarithmic decline of temperatures in the upper part of the water column in terms of the Beer-Lambert Law and the infrared absorption characteristics of water.

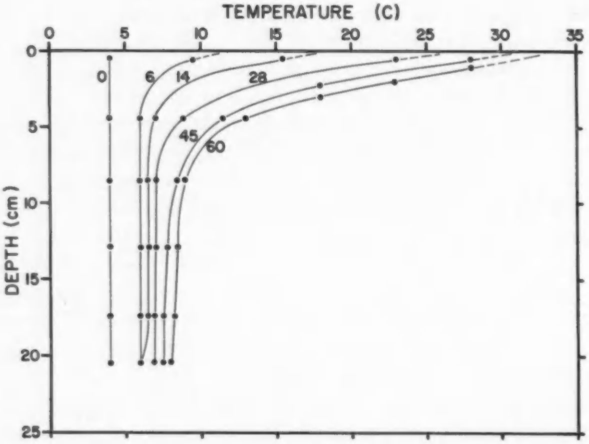


Fig. 1. Distribution of temperature with depth as a function of time in an uninsulated aquarium heated by a single 250-w infrared bulb located 20 cm above the water surface in the absence of wind. The numbers beside the curves give the time in minutes from the start of the experiment.

Powdered dye crystals are now lightly and evenly spread over the water surface, most dissolving in the uppermost 2 cm of the water column with a few trails into the bottom in order to follow water movements in the hypolimnion. A light and alternating wind is used to create a homogeneous distribution of dye in the uppermost 5 cm of the water column. A typical temperature profile at this time is shown in curve *a* of Fig. 2. The importance of the wind in creating the tripartite structure of an epilimnion, thermocline, and hypolimnion is thus quickly appreciated.

---

[2] Each bottle of dye used must be tested individually for its applicability to the system.

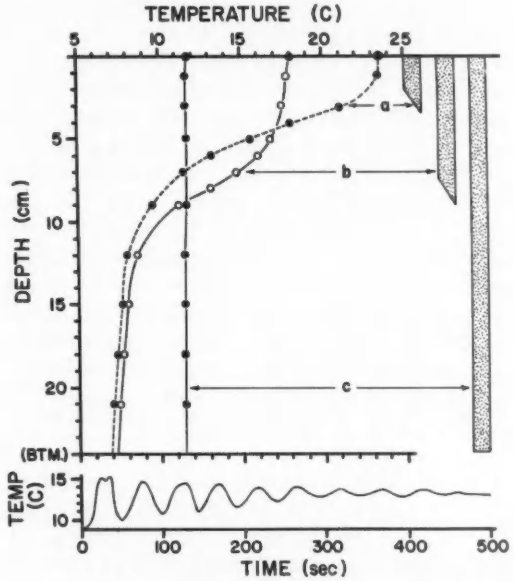


FIG. 2. Temperature distribution in a holomictic lake model after heating a water mass initially 4 C throughout in the absence of wind: *a*, after a light oscillating wind; *b*, after forced oscillations of an internal seiche; *c*, after complete mixing by a strong wind. The stippled area to the right shows the depth distribution of added dye. The insert below shows the time fluctuation of water temperatures at a fixed depth in the region of the thermocline during the oscillations of an internal seiche (determined at 5-sec intervals with a thermistor thermometer).

After recording the distribution of temperature and dye, an internal seiche is generated by a series of forced oscillations from the wind. (Some practice may be required to produce a good uninodal seiche.) The period of the seiche is determined either by timing vertical displacements of coloured water at one end of the basin or by placing a thermistor thermometer in the region of the thermocline (see bottom insert for Fig. 2). After the system has come to rest the distribution of temperature and dye is again recorded (see curve *b* of Fig. 2) and the process repeated. The distribution of density within the system will have changed in the interval between the two seiches, and likewise the periodic times. The observed periods are compared with those calculated from the equation for a uninodal internal seiche in a rectangular basin (see Hutchinson, 1957, p. 336), and the students are required to explain in physical terms why the periods differ in the two cases.

The entire water column is finally mixed with a strong wind, resulting in a uniform distribution of temperature and dye as shown in *c* of Fig. 2. Alternatively, the final mixing can be achieved by convection cells generated from masses of ice cubes gently lowered into the surface water. Cold, finger-like projections of coloured water will be seen descending into the uncoloured region below. These rise as they are warmed by the lowermost waters, others descending elsewhere until the entire aquarium becomes filled with dye.

As subsidiary calculations, the class is required to chart the density profiles in the water column for situations comparable to those in *a* and *b*, or *a* and *c*, in Fig. 2. (It is assumed for simplicity that the aquarium contains pure water.) From the smoothed curves so generated the density difference between the top and bottom of each 1-cm depth interval is plotted separately to delineate regions of maximal thermal resistance to mixing. In addition, the overall stability of the model lake is calculated according to Schmidt (see Hutchinson, 1957, p. 510). Finally, using a temperature profile similar to *a* or *b* of Fig. 2, the summer heat income of the model lake is calculated relative to a water column with a temperature of 4 C throughout (Hutchinson, 1957, p. 494).

Experiment II. Model of a tropical lake.— A similar procedure to the above is repeated for a tropical lake model in which the initial temperature is 25 C throughout. This is instructive in demonstrating the high stability that can result from small temperature differences at elevated temperatures. Internal seiches have, in fact, been generated with a temperature differential of only 1 C (26 C–27 C). The effect of occasional cool periods on water circulation can be shown by placing a high capacity cold source above the aquarium.

Experiment III. Model of a meromictic lake.— Approximately 1 hr is required to set up this model. The aquarium is first filled two-thirds full with a mixture of water and enough ice to persist for half an hour. The monimolimnetic water consists of a 0.3% NaCl solution at room temperature, to which dye has been added. The solution is introduced by gravity from a 2-gal reservoir via flexible tubing into an L-shaped glass tube (1 cm diam, 35 cm long, and with a short unpolished end about 4 cm long). After extrusion of air bubbles, the glass tube is lowered into the aquarium at a slant to avoid mixing, and clamped in position with the short horizontal piece resting on the bottom at one end of the aquarium. Flow is adjusted by means of a screw clamp taking care not to exceed the critical velocity for laminar flow. (This in itself is an interesting exercise for the student.) The flow can be increased as the aquarium fills. Approximately 40 min is required for the addition of a

0.3% salt solution, a slightly shorter time for a 3% solution, and 4–6 hours for a 0.03% solution.

When the aquarium is full, the flow is shut off, the tube carefully removed with minimal mixing, and the temperatures recorded (see Fig. 3, curve *a*).

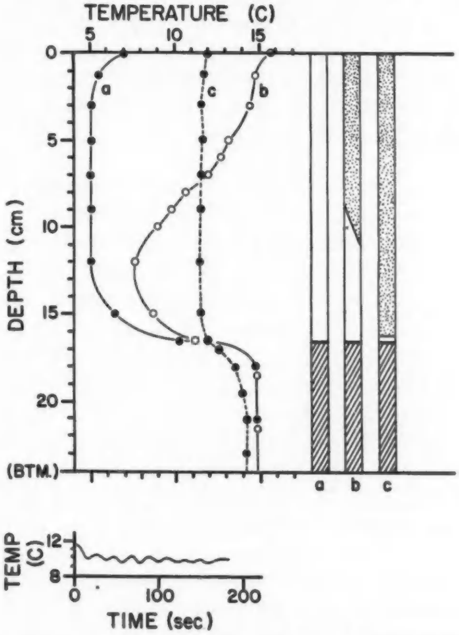


FIG. 3. Temperature distribution in a meromictic lake model: *a*, initial situation after influx of monimolimnetic water into the aquarium; *b*, after a 40-min heating period with one 250-w infrared lamp located 20 cm above the water surface, followed by an oscillating wind; *c*, after complete mixing of the upper, non-saline waters by a strong wind. The stippled area at the right shows the distribution of dye in the epilimnion, and the area with slanted lines, the distribution of dye in the monimolimnion. The insert below shows the fluctuation of water temperatures at a fixed depth in the region of the thermocline during the oscillations of an internal seiche (determined at 5-sec intervals with a thermistor thermometer). Note the shorter period of the seiche as compared with Fig. 2.

The infrared lamps are turned on at this time and the water heated for 20-30 min in the absence of wind. Powdered dye is then sprinkled over the surface following the same procedure as outlined in Experiment I. An example of the thermal structure after initial mixing and forced oscillations of an internal seiche is shown in curve *b* of Fig. 3; and that after complete mixing of the non-saline waters by a strong wind in curve *c* of Fig. 3. It is apparent from the latter that some exchange of heat has taken place across the chemocline. The lower insert of Fig. 3 shows temperature oscillations at a fixed depth in the region of the thermocline.

The experiment is completed with a demonstration of the effectiveness of bubbles in mixing water masses separated by a density barrier at some depth. This is accomplished by dropping a large effervescent tablet enclosed in heavy wire screen into the aquarium.[3] The violent turbulent motion carries water of the differentially stained monimolimnion into the upper water mass. Virtually complete mixing can be brought about by repetition and the changes followed spectrophotometrically if desired.

Experiment IV. Continuous sun and wind.— In the above experiments the actions of sun and wind were separated for instructional reasons in one case and as matter of convenience in the other two. In this experiment the wind source is held in a fixed position and activated at the same time as the sun. The wind source is initially positioned by trial to produce rather slow but detectable currents in the bottom water when the temperature is 4 C throughout. (It is helpful for this purpose if the water contains some small particles of dust or other material.) The lights and wind are turned on and temperatures measured at 10-min intervals over a 40-min period. Results from one such experiment are shown by the solid lines in Fig. 4A. The lights are then turned off and the wind allowed to continue unchanged over an additional 40-min period (broken lines in Fig. 4A).

For comparative purposes a second experiment is conducted with everything unchanged except that a stronger wind is used. Part of the water in the aquarium is replaced by sufficient ice to bring the temperature back to 4 C, and the water surface adjusted to its previous level. The wind source is advanced to a position that will cause complete circulation throughout a 40-min heating period. Typical results are shown in Fig. 4B.

The class is required to calculate eddy conductivity coefficients for the case with incomplete circulation, and to prepare a table listing the heat gained (cal cm^{-2} for each 10-min interval) for both cases. The latter exercise is useful in showing the importance of the wind and thermal stratification in determining the uptake of heat by a lake.

As individual laboratory exercises, students may profitably be asked to mimic other phenomena of limnological interest: effect of sills and other bottom configurations on water circulation; generation of multiple thermoclines; geostrophic effects on currents (with the apparatus on a slowly rotating laboratory stool); density currents and the phenomenon of La Bataillère (see Hutchinson, 1957, p. 296); and so on. These have all been tested with success.

Some thought has been given to the development of a system that will maintain a given thermal stratification over a period of days or even weeks; however, no experimental work has been attempted as yet. The development of such a system would permit simulated lacustrine observation of the growth,

---

[3] I am indebted to Mr Dean Arnold for this suggestion.

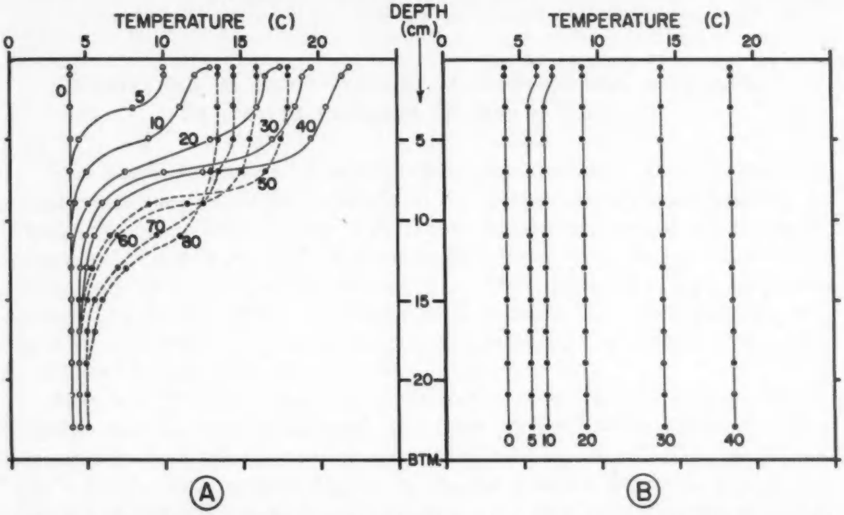


FIG. 4. Distribution of temperature as a function of time in an insulated aquarium with constant wind and two 250-w infrared bulbs located 8 cm above the water surface. A, moderate wind. The solid lines show temperatures observed during the initial heating period; and the broken lines, the temperatures observed at various intervals after the lamps were turned off, 40 min from the start of the experiment. B, same, but with a stronger wind. The numbers refer to minutes elapsed from the start of the experiment. Note the progressive descent of the inflection point of the thermocline in A, both during and after heating. Also, compare the rise of only 1 C in the hypolimnion in this insulated aquarium to the rise 3–5 C shown for uninsulated aquaria in Fig. 1–3.

movement, and reproduction of microorganisms. With the introduction of actively decaying sediment and a variable flow through the system the model could encompass most of the biological and biochemical complexities of lakes, well beyond the physical phenomena described herein.

The purpose of this note is to bring the model to the attention of those involved in teaching limnology, ecology, and general biology. Models have immense educational value in that they allow the student to experiment rather than merely observe. The use and further development of the system described here could do much to create a general sense of awareness and limnological intuition in both students and teachers alike.

I am indebted to Mr T. Cleugh for assistance during the terminal stages of this investigation.

Fisheries Research Board of Canada
Freshwater Institute, Winnipeg, Man.

J. R. VALLENTYNE

Received for publication August 1, 1967.

REFERENCES

HUTCHISON, G. E. 1957. A treatise on limnology. Vol. I. xii + 1015 p. John Wiley & Sons, New York.

Wintering of Pilot Whales, *Globicephala melaena*, in Newfoundland Inshore Waters

The North Atlantic pilot whale, *Globicephala melaena* (Traill), has been recorded southwards to New Jersey with a single extralimital stranding at Virginia (Paradiso, 1958). Ulmer (1961) reports that New Jersey is the northernmost limit of the tropical *G. macrorhyncha*, where it is the more abundant species; the only positive *G. melaena* from New Jersey are two specimens examined by Ulmer (1961). The range of *G. melaena* is continuous across the North Atlantic and in the east the zone of interchange apparently lies farther south (see Davies, 1960; Brown, 1961).

Although it often occurs in coastal waters of the Gulf of Maine (W. E. Schevill, personal communication), it is only in the Newfoundland area that the northern pilot whale (here known by the more apt vernacular name "pothead") occurs inshore with regularity in the western Atlantic. During the period from July to October or early November *G. melaena* is the most abundant cetacean in Newfoundland waters (Sergeant and Fisher, 1957). The migration inshore follows closely that of the ommastrephid squid, *Illex illecebrosus* (Lesueur), which is the preferred food of pilot whales in the area (Sergeant, 1962); the offshore migration in late fall also coincides with that of the squid.

Winter occurrences in the Newfoundland area.— Mr Clayton Barbour, technician at the St. John's Biological Station, reports sighting a herd of about 25–30 pilot whales off Horsechops in Trinity Bay on January 9, 1967. Surface temperature at the time was 2.6 C (at 48°12′15″N, 53°05′00″W).

On February 14, 1967, fishermen drove a herd ashore at Chapel Arm, Trinity Bay, and Mr William Barrett of Arctic Fishery Products Limited reports that 63 were taken; since several are known to have escaped, the herd may have comprised 80 or more animals. Mr Barrett also reports that a herd, presumably this one, had been sighted in the bay several times during the winter and he had observed it in Dildo Arm during the previous week. (Surface temperature on March 5 was −1.1 C at 47°50′15″N, 53°36′30″W.)

When the author arrived at Chapel Arm on the afternoon of February 15 flensing operations were already nearing completion. Nevertheless some useful data were obtained. Standard body lengths were estimated by eye from the carcasses, most of which had the head and flukes removed. Although size data (Table I) are approximate they do indicate that the herd included a full range of lengths from young juveniles to specimens approaching maximum adult size. The author estimated lengths of 61 animals; likely the other two were small and the whole carcasses were taken to the plant for processing.

Several foetuses were found and these were measured (head beyond tip of jaw to fluke notch) using a centimetre tape. Lengths (in centimetres) were: 69, 51, 73, 136, 87 + (head missing). Mr Barrett reported that he noted foetuses from about 1–6 ft (30–183 cm) in length in specimens he examined.

J. Fish. Res. Bd. Canada, 24(11), 1967.
Printed in Canada.

TABLE I. Estimated standard lengths of pilot whales driven ashore at Chapel Arm, February 14, 1967.

Length (*ft*)	Number
6–7	7
8–9	7
10–11	7
12–13	14
14–15	18
16–17	3
18–19	5

The author examined three stomachs; one was empty; the other two contained vertebrae and other bones of Greenland halibut, *Reinhardtius hippoglossoides*; no squid were found. Mr Barrett reported finding no food in any of about six stomachs he examined.

Mr Barrett also reports sighting a large herd, comprising possibly as many as 200 animals, at Dildo in January of 1951. These swam into the arm and retreated immediately; no attempt was made to chase them. One further sighting may be noted. The Staff Newsletter, issued by the Canada Department of Fisheries at St. John's, reported (February 1964) that a small herd of pilot whales was seen in Bonavista harbour during the latter part of February 1964.

Discussion.— Little is known of the migratory habits and wintering areas of this economically important cetacean. The earliest date recorded by Sergeant and Fisher (1957) for the arrival of pilot whales on the Grand Bank is June 27 both in 1953 and 1954, although a herd was sighted on the southern part of the Grand Bank during the first week of January in 1953. The earliest record from Newfoundland coastal waters is June 26, 1954 and the latest sighting in Trinity Bay during the period 1951–55 was on November 10, 1954.

Sergeant and Fisher (1957) recorded sightings of pilot whales at weather station D (east of the Grand Bank, 43°50′–45°30′N, 40°44′–41°21′W during the months September, October, December, January, February, June, and July. They also report two records which they regard as doubtful; these sightings were obtained in March from the Labrador Sea. Brown (1961) showed that pilot whales are found over deep water across the North Atlantic throughout the year.

Mr William E. Schevill reports (personal communication) three winter (December–March) pilot whale sightings made on board vessels of the Woods Hole Oceanographic Institution in the area 39°42′–41°00′N, 70°25′–70°53′W.

The author also sighted four large *Globicephala* sp. at 38°44′N, 73°04′W, on April 2, 1967. However, these may have been *G. macrorhyncha*.

Jensen (1939) reported a single overwintering near Godthaab in 1931–32.

Sergeant (1962) believes that the main wintering area of the Newfoundland stock is in the waters of the North Atlantic Current, east of the Grand Bank.

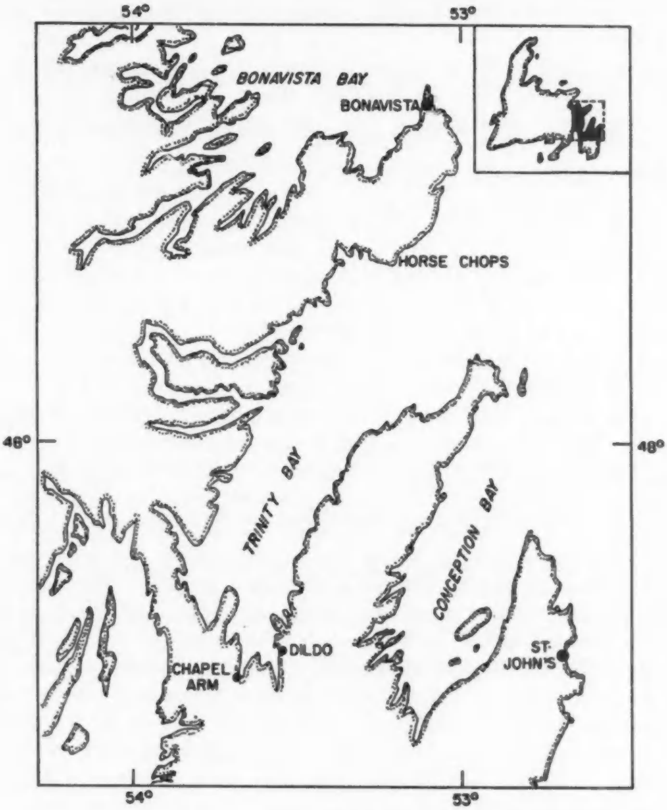


FIG. 1. Places in Newfoundland mentioned in the text.

A concerted tagging program is required to elucidate this problem. A possible method is large scale tagging inshore, using radio tags, with subsequent aerial oceanic surveys in winter. This approach may be inviting in spite of difficulties caused by sea surface interference.

These constitute the first winter records of the pilot whale from Newfoundland inshore waters. Since the sightings are of entire herds rather than isolated strays they are of some ecological interest. The herd driven at Chapel Arm is a definite case of overwintering since several previous sightings had been made earlier in the winter.

The records indicate great flexibility in diet and temperature tolerance. Sergeant (1962) found only squid (*Illex illecebrosus*) in stomachs of pilot whales examined 1951–56; cod (*Gadus morhua*) were found in some stomachs in 1957–58 when squid were scarce inshore. During the season when pilot whales and squid normally occur, inshore surface temperatures range from about 5 to 16 C.

I am indebted to W. E. Schevill, Woods Hole Oceanographic Institution, and D. E. Sergeant, Fisheries Research Board of Canada, Arctic Biological Station, Ste. Anne de Bellevue, Que., for critically reading the manuscript.

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

M. C. MERCER

Received for publication July 17, 1967.

REFERENCES

BROWN, S. G. 1961. Observations on pilot whales in the North Atlantic. Norwegian Whaling Gaz., **50**(6): 225–254.

DAVIES, J. L. 1960. The southern form of the pilot whale. J. Mammal., **41**: 29–34.

JENSEN, A. S. 1939. Concerning a change of climate during recent decades in the arctic and subarctic regions . . . and contemporary biological and geophysical changes. Kgl. Danske Vidensk. Selskab. Biol. Medd., **14**(8): 1–75.

PARADISO, J. L. 1958. The common blackfish in Virginia coastal waters. J. Mammal., **39**: 440–441.

SERGEANT, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Bull. Fish. Res. Bd. Canada, No. 132. 84 p.

SERGEANT, D. E., AND H. D. FISHER. 1957. The smaller Cetacea of eastern Canadian waters. J. Fish. Res. Bd. Canada, **14**(1): 83–115.

ULMER, F. A. 1961. New Jersey's whales and dolphins. N.J. Audubon Soc., **16**(3): 80–93.

Fecundity and Length–Weight Relationship in Lingcod

Occasional determinations of fecundity in lingcod, *Ophiodon elongatus* Girard, were made during a life history study in the waters of southern British Columbia from 1937 to 1942.

Evidence from tagging (Chatwin, 1956b) shows that in the Strait of Georgia lingcod movements are very restricted or that migrations tend to be from and to a home reef. Fishing experience and the habits of hand-line fishermen support the tagging evidence. In some areas within the range there appear to be freely moving parts of the population. As a result of its non-migratory tendency, lingcod in areas closed to commercial fishing develop under conditions of population density different from those in unrestricted areas.

Lengths were measured from the tip of the closed lower jaw to the "fork" of the tail to the closest centimetre on a measuring board. Fish were weighed in a mesh sling suspended from an adjusted spring balance suspended from the boom of a fishing boat or other convenient place. In many cases, interpolations were necessary to allow for wind effects and movements of fish and boat. The dial of the scale was calibrated in 2-oz (57-g) intervals and much number preference is evident. Many fish weights can be regarded as accurate only to the closest pound (0.454 kg). Both ovaries from the ripening fish were removed, preserved in formalin, and weighed in the laboratory. Composite samples from several regions in the ovary were weighed, the large ova were counted, and the number of ripening eggs per fish calculated.

Complete sets of data are available for 42 fish sampled in the following years: 1938, 4; 1941, 32; 1942, 6. The 1942 samples were entirely from Saanich Inlet where commercial fishing was never allowed and where fish were notably abundant and easy to catch on hand lines. In addition, length and fecundity data are available for 13 1940 fish. Aside from 1942 all fish were hand-lined on fishing grounds of the Strait of Georgia. All fish were caught in December and January.

Regression equations based on logarithms of data are given as calculated and as converted to natural numbers, with interpretations below:

Egg number and fish length (*Fig. 1*).— N = egg number; L = length mm; Y = log egg number; X_1 = log length. For all data:

$$Y = 3.0011\ X_1 - 3.5491$$

$$N = \frac{1}{3541} L^{3.0011}.$$

To facilitate comparisons the calculations were made for all the data less those for 1940

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

$$Y = 2.9894 X_1 - 3.5007$$

$$N = \frac{1}{3167} L^{2.9894}.$$

The sum of squares of deviations for the regression is 0.2992 for data excluding 1940. The standard errors of the slope and intercept for the total sample are 0.28 and 0.012 respectively; thus the difference in slope is well below the significance level and that in the intercept is barely significant at the $P = 0.05$ level.

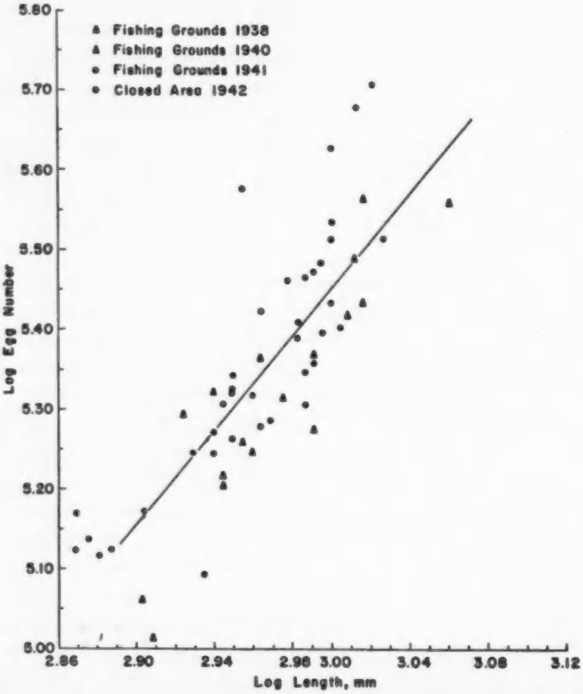


FIG. 1. Regression log egg number on log length (mm) for lingcod. Log egg number = 3.0011 log length − 3.5491.

Data for 1942 show egg number for length to be significantly lower than for 1941. The variance ratio F = 10.03. For the same number of degrees of freedom, 1 and 33 and $P = 0.01$, F = 7.47 (Snedecor, 1956, p. 244). This suggests that crowding may affect fecundity, but the conclusion must be accepted with caution as four sets of observations for 1938 also show egg numbers that are below the regression line. Also Fig. 1 suggests that the logarithmic transposition may not give an exact linear relationship.

Egg number and fish weight.— W = weight in pounds; X_2 = log weight. There are no weight data for 1940.

$$Y = .8498\, X_2 + 4.2099$$

$$N = 16210\, W^{.8498}$$

sum of squares .0845.

Egg number and fish weight minus ovary weight.— As the most fecund fish might be expected to have the heaviest ovaries, there is a possibility of bias in relating total fish weight to fecundity. The expectation is not supported. W_o = fish weight minus ovary weight. X_3 = log fish weight minus ovary weight.

$$Y = .8731\, X_3 + 4.2285$$

$$N = 16920\, W_o^{.8731}$$

sum of squares .0675. The W_o relationship evidently provides the best fit.

Graphing shows no indication of difference between 1942 and 1941 data. Evidently fecundity is more closely related to weight than to length. However, graphing 1938 data shows all four egg numbers still to be well below the regression line.

Plots of Y and X_3 dished upward slightly and led to exploration of the linear relationship leading to the fitted line

$$N = 10578\, W_o + 18966.$$

Objective comparisons of goodness of fit of the two lines have not been made. On the whole, they seem to be of about equal merit. Graphing suggests preference for the linear relationship as the logarithmic fit leaves the last five plotted points increasingly above the calculated line.

Weight and length.— X_2 = log weight; X_1 = log length (Fig. 2)

$$X_2 = 3.6558\, X_1 - 9.4845.$$

The length–weight relationship for ripening female lingcod in the Strait of Georgia was approximately

$$W = 10^{-10} \times 3.277\, L^{3.6558}.$$

Lingcod from the crowded area were significantly lighter than fish of the same length from exploited areas. Variance ratio $F = 8.76$, and again for $P = 0.01$, and degrees of freedom 1 and 33, $F = 7.47$.

This is not believed to be a product of seasonal variation. Observations of fishermen support this conclusion. Fish in newly discovered concentrations are notably poor and "all head."

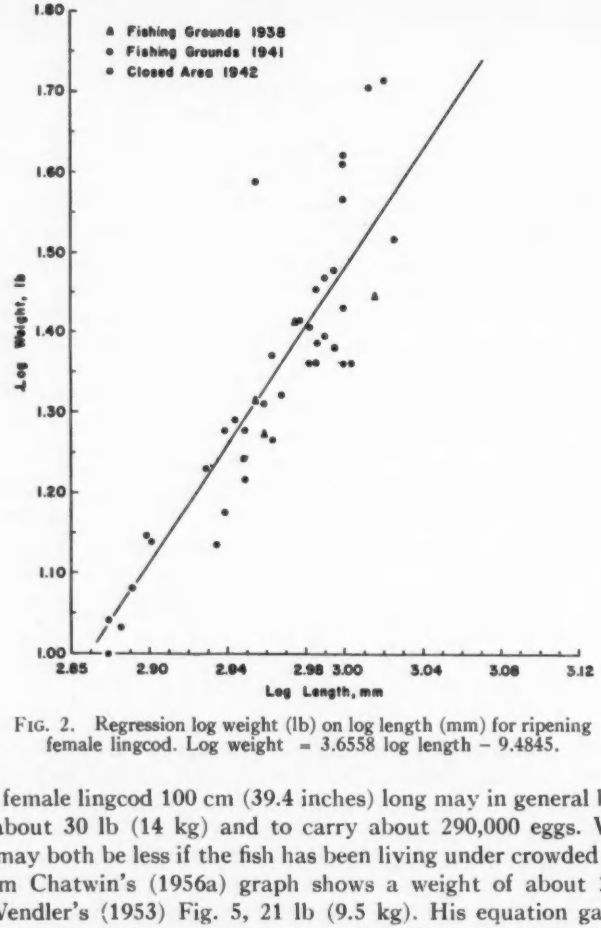


FIG. 2. Regression log weight (lb) on log length (mm) for ripening female lingcod. Log weight = 3.6558 log length − 9.4845.

A full female lingcod 100 cm (39.4 inches) long may in general be expected to weigh about 30 lb (14 kg) and to carry about 290,000 eggs. Weight and fecundity may both be less if the fish has been living under crowded conditions. For 100 cm Chatwin's (1956a) graph shows a weight of about 23 lb (10.5 kg) and Wendler's (1953) Fig. 5, 21 lb (9.5 kg). His equation gave trouble. Their data are based, on presumably spent April and May fish. Clemens and Wilby (1961) for 34 inches (86 cm) and 46½ inches (118 cm) cite 170,000 and 476,000 eggs. The equation developed here gives about 185,000 and 470,000 eggs.

The assistance is acknowledged of Mr Soren Vollmers, the fisherman whose knowledge of fish and their ways made this work possible, and of Mr K. R. Allen whose knowledge and skill in statistical procedures produced the mathematical analysis.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

J. L. HART

Received for publication May 15, 1967.

REFERENCES

CHATWIN, B. M. 1956a. Age and growth of lingcod (*Ophiodon elongatus*). Fish. Res. Bd. Canada, Pacific Progr. Rept. No. 105. p. 22–26.

1956b. Further results from tagging experiments on lingcod. Ibid., No. 107. p. 19–21.

CLEMENS, W. A., AND G. V. WILBY. 1961. Fishes of the Pacific Coast of Canada. Bull. Fish. Res. Bd. Canada, No. 68. 443 p.

SNEDECOR, G. W. 1956. Statistical methods, 5th ed. Iowa State Univ. Press, Ames, Iowa. 534 p.

WENDLER, H. O. 1953. Length–weight relationships of the ling cod. Wash. Dept. Fish., Fish. Res. Papers, **1**(1): 25–32.

Computer vs. Manual Calculations of Temperatures and Depths[1,2]

This note compares ocean temperatures and depths from 484 stations (three cruises, 1961–63) calculated manually with the values calculated by computer. The manual correction of the temperatures involved graphical, or nomogram, aids; depths were calculated manually by fitting a smooth curve to an array of "thermometric points" given by pairs of protected-unprotected thermometers (LaFond, 1951).

The computer program itself has been described elsewhere (Keyte, MS, 1966). Briefly, it contained the thermometer correction formulas of Hansen (1934) and Keyte (1965) for protected and unprotected thermometers respectively, and it used a fourth-order polynomial regression on the thermometric points, the order being decreased if there were fewer than six points.

Cruise 1 in 1961 had 138 stations, cruise 2 in 1962 119 stations, and cruise 3 in 1963 227 stations. Most of the 484 stations sampled deeper than 1000 m. There were 9038 temperatures from the protected thermometers, and 8981 depths; 57 depths were not compared because of pre- or post-tripping of the hydrographic cast. All temperatures were rounded to two decimal places, and depths rounded to the nearest metre.

Temperature comparisons.—In the absence of error, the temperatures calculated by hand (T_h) and by computer (T_c) should be identical; that is, for each comparison,

$$\delta T \equiv T_c - T_h = 0.$$

Table I shows the frequency distribution of the quantity δT that was actually found. Note that class intervals are a hundredth of a degree up to $\delta T = \pm 0.10$ C, a tenth of a degree thereafter.

A strange feature of Table I is that generally there are more negative than positive δT in comparable classes. No clear reason for this disproportion was found: the correction graphs used in the manual reductions appeared correctly drawn, and certainly any optical illusion generated by the slanted nomograms on the graphs would contribute only to the $\delta T = \pm 0.01$ C class. Nor does manual cumulative rounding error apply here, because only one thermometer was attached to each sample bottle and each thermometer was read only once.

There were four discrepancies as large as one degree between computer and manual values (Table I); all four cases were traced to error in transcribing in the manual work. In fact, all $|\delta T|$ greater than 0.02 C were individually investigated and were found to arise from human error in the manual reductions.

---

[1] Contribution No. 78 from the Bedford Institute of Oceanography.
[2] Contribution No. 1904 from the Woods Hole Oceanographic Institution.

TABLE I. Frequency distribution of δT (difference between temperatures calculated by computer and by hand); 484 stations.

δT (C)	−.91 to −1.0	−.81 to −.90	−.71 to −.80	−.61 to −.70	−.51 to −.60	−.41 to −.50	−.31 to −.40	−.21 to −.30	−.11 to −.20	−.10	−.09	−.08	−.07	−.06	−.05	−.04	−.03	−.02	−.01	0	+.01	+.02	+.03	+.04	+.05	+.06	+.07	+.08	+.09	+.10	+.11 to +.20	+.21 to +.30	+.31 to +.40	+.41 to +.50	+.51 to +.60	+.61 to +.70	+.71 to +.80	+.81 to +.90	+.91 to +1.0
No. of cases	3		1	1	1	2	3	2	2	8	1	1	1	9	7	6	18	89	984	7358	374	79	13	38	21	6	1		1	3	2	1	1						1

However, a large percentage of manual values agreed exactly with the computer. The error rate in human reductions varied from 12% to 25% in the individual cruises if an error is defined to be $|\delta T|$ 0.01 C or greater (Table II). The rate dropped to a maximum of only 5%, however, if an error is defined to be $|\delta T|$ 0.02 C or greater.

TABLE II. Error rates in manual temperature reductions for the three cruises.

	No. of cases	Occasions where $|\delta T| \geq 0.01$ C	Error rate (%)	Occasions where $|\delta T| \geq 0.02$ C	Error rate (%)
Cruise 1 (138 stations, 1961)	2427	301	12	41	2
Cruise 2 (119 stations, 1962)	2075	248	12	36	2
Cruise 3 (227 stations, 1963)	4536	1131	25	245	5
All cruises (484 stations) Total	9038	1680	19	322	4

Depth comparisons.—Let the quantity δZ be defined as the difference between accepted computer-calculated and hand-calculated depths:

$$\delta Z \equiv Z_c - Z_h.$$

In tabulating the δZ, three arbitrary layers of water depth, each with its own class interval, were chosen: a shallow layer, 0–1000 m, with δZ every ±1 m; a middle layer 1001–2000 m, δZ every ±2 m; and a deep layer 2001 m and greater, δZ every ±5 m.

Table III shows the 8981 depth comparisons of all three cruises, distributed among the three layers. The "class total" is the sum of the number of cases in each depth interval, and the "per cent of total" is this sum reduced to a per cent of the layer total. The computer and manual depths correspond closely: 97.5% of shallow depths agree to ±5 m, 96.1% of middle depths to ±10 m, and 98.6% of deep depths to ±25 m. On the other hand, the computer did find many errors in the manual work, the worst being nine transcription errors of 100 m magnitude (not shown in Table III).

An asymmetry of the δZ distribution, similar to that for δT, may be noted in Table III: here the peaking is on the positive side of zero. Again, no convincing explanation was found.

Conclusion.—In the data from the 484 stations manual errors as large as one degree in temperature corrections and 100 m in depth calculations were found by a computer. Whereas temperatures are routinely processed to the

TABLE III. Frequency distributions of δZ (difference between depths calculated by computer and by hand); 484 stations.

Shallow layer, 0–1000 m										
δZ (*m*)	< −15	−15 −14 −13 −12 −11	−10 −9 −8 −7 −6	−5 −4 −3 −2 −1	0	+1 +2 +3 +4 +5	+6 +7 +8 +9 +10	+11 +12 +13 +14 +15	> +15	
No. of cases	3	2 3 4 3	3 8 10 21 30	50 97 179 351 832	2958	1034 622 321 150 56	26 21 11 8 1	2 3 1	9	
Class total	3	12	72	1509	2958	2183	67	6	9	6819
Per cent of total	0.0	0.2	1.1	22.1	43.4	32.0	1.0	0.1	0.1	100.0
Middle layer, 1001–2000 m										
δZ (*m*)	< −30	−30 −28 −26 −24 −22	−20 −18 −16 −14 −12	−10 −8 −6 −4 −2	0	+2 +4 +6 +8 +10	+12 +14 +16 +18 +20	+22 +24 +26 +28 +30	> +30	
No. of cases	5	2 1 1 1	 1 1 1 4	9 31 27 57 97	95	285 263 111 74 18	8 5 3 1	3 1 1	3	
Class total	5	5	7	221	95	751	17	5	3	1109
Per cent of total	0.5	0.5	0.6	19.9	8.5	67.7	1.5	0.5	0.3	100.0
Deep layer, 2001 m and greater										
δZ (*m*)	<−75	−75 −70 −65 −60 −55	−50 −45 −40 −35 −30	−25 −20 −15 −10 −5	0	+5 +10 +15 +20 +25	+30 +35 +40 +45 +50	+55 +60 +65 +70 +75	> +75	
No. of cases	4		1 1 2	8 9 41 86 204	71	428 159 21 7 5	3 2 1			
Class total	4	0	4	348	71	620	6	0	0	1053
Per cent of total	0.4	0.0	0.4	33.0	6.7	58.9	0.6	0.0	0.0	100.0

second decimal place, depths to a metre cannot be known by the reversing thermometer technique, so computer-manual depth comparisons are not quite as meaningful as temperature comparisons. Nevertheless the computer has three advantages over manual depth calculations: (1) it is faster (once the raw data are coded); (2) it is more precise, i.e. gives reproducible answers; and (3) it can be programmed to consider more variables than the manual method is able to do, and should therefore be able to produce a more accurate depth curve than is possible by hand.

It must be stressed that the preparation of the raw data for the computer, being itself a manual process, had to be carefully checked for the type of transcription errors seen so often in the manual work.

The cruise data on which the above investigation was based were made available to me through the courtesy of the Woods Hole Oceanographic Institution, while I was on leave of absence from the Canada Department of Energy, Mines and Resources. I wish to thank Mr A. R. Miller of that Institution for many personal kindnesses during the course of this study; Mrs Jacqueline Webster for invaluable help in writing the computer program; and Mrs Carol Reynolds for the laborious checking of the tables.

This work was supported by National Science Foundation Grant GP-821.

Dept. of Energy, Mines and Resources
Bedford Institute of Oceanography
Dartmouth, N.S.

F. K. KEYTE

Received for publication February 24, 1967.

REFERENCES

HANSEN, W. 1934. Bermerkungen zu den Korrektionsformeln fur das Tiefsee-Umkippthermometer. Ann. Hydrog. Marit. Meteorol., **62**: 145–147.

KEYTE, F. K. 1965. On the formulas for correcting reversing thermometers. Deep-Sea Res., **12**: 163–172.

MS, 1966. A computer program to reduce and edit hydrographic station data. Bedford Institute of Oceanography, Computer Note 66-5-C, Dartmouth, Nova Scotia.

LAFOND, E. C. 1951. Processing oceanographic data. U.S. Navy Hydrographic Office, Washington, D.C. 114 p.

Insect Molt-Hormone Activity of an Extract of the Japanese Yew (*Taxus cuspidata*)

Recent reports show that some plants have ecdysone-like compounds in high concentrations (Galbraith and Horn, 1966; Kobayashi et al., 1967; Nakanishi et al., 1966; and T. Takemoto, personal communications with Dr A. Saito of this laboratory). These compounds show substantial activity in insect molt-hormone bioassays (Kobayashi et al., 1967). As far as the authors are aware, none of the plants reported to contain these compounds are indigenous to North America. As part of an attempt to obtain ecdysone or its analogues in quantity for biological studies on crustacea, a preliminary survey of locally available plants has been started. By far the most potent plant extract found to date came from the Japanese yew (*Taxus cuspidata*), a common shrub.

A sample (206 g wet weight) of whole yew branches, which had been stored for 3 days at −18 C, was extracted by a procedure known to remove and concentrate insect ecdysones. With minor modifications the procedure was that described by Kaplanis et al. (1966a). The plant material was chopped, blended in 412 ml acetone–ethanol (1:1), and filtered by suction. The solids were extracted as above and finally washed with one-half the above volume of solvent mixture. The combined, very dark solutions were evaporated to near dryness with a rotary evaporator (maximum bath temperature, 40 C) and suspended in 206 ml water. Anhydrous sodium carbonate was added to the suspension to make a 2% (w/v) solution. The aqueous suspension was extracted once with an equal volume of redistilled butanol and twice with one-half that volume. The combined butanol fractions were washed with several one-tenth volumes of water until the washings were approximately neutral and the butanol evaporated as above. The butanol extract residue was dissolved in 110 ml of 70% methanol and extracted six times with equal volumes of *n*-hexane. The combined hexane phases were back-washed with 66 ml 70% methanol. The combined 70% methanol fractions were evaporated to dryness as before to yield 4.030 g of green–black residue. For the insect bioassay the residue was suspended in 10% ethanol to give a final concentration of 100 mg/ml. Subsequently, appropriate dilutions of the original solution were then made with 10% ethanol as indicated.

The housefly bioassay used was that described by Kaplanis et al. (1966b) with minor modifications suggested by the most recent insecticide testing procedure (Anon., 1966). The animals were grown in 30-C incubators with uncontrolled humidity.

Preliminary testing was conducted with small numbers (5–8) of animals to establish approximate activity levels. These tests were then followed by tests with larger groups of animals in attempts to match the response to the yew extracts with that elicited by authentic 20-hydroxyecdysone. Table I

J. Fish. Res. Bd. Canada, **24**(11), 1967.
Printed in Canada.

TABLE I. A housefly bioassay comparison of 20-hydroxyecdysone activity with that of the yew extract

Sample	Quantity injected (μg)	Per cent pupation[a] 1st test	2nd test
Control	0	18	18
20-Hydroxyecdysone	0.002	47	45
	0.005	68	68
Yew extract	0.2	43	47
	0.3	75	53

[a]Each number represents the average response of 10 animals.

shows the relative amounts of crude yew extract required to match approximately the housefly bioassay activity of 0.002 and 0.005 μg of authentic 20-hydroxyecdysone. Controls were injected with 3 μl 10% ethanol. Ten animals were used in each test.

Kaplanis et al. (1966a, b) considered 0.005 μg of 20-hydroxyecdysone to be approximately equivalent to 1 housefly unit (HFU). About 0.3 μg of crude yew extract residue showed equivalent activity. The response to the yew extract was not strictly proportional to concentration; the more dilute samples when injected tended to give a greater response per μg than the more concentrated. Oddly, the most concentrated yew extract solution tested was inactive in the bioassay whereas greater dilutions gave reactions approaching maximum pupation. The preparations exhibited much the same disproportionate response even after chromatography, which suggested self-inhibition was a likely cause.

Within the limitations of the bioassay one can estimate that the whole yew extract from 206 g fresh tissue must contain activity equivalent to 67 mg of 20-hydroxyecdysone or approximately 13,000,000 HFU. To prepare this much active material from the hornworm (a "rich" source) would require 22 kg of pupae at the time of optimum hormone titer (Kaplanis et al., 1966a).

In addition to raising interesting questions as to the function of compounds with ecdysone activity in plants, the present study, like those of other authors mentioned, will help to make ecdysone analogues readily available for biological studies on insects and crustaceans.

We acknowledge with thanks the advice and assistance of Dr D. R. Idler. We wish also to thank Mr G. J. Power, director of the Public Gardens, Halifax, N.S., for supplying plant samples, and in particular to thank Dr J. N. Kaplanis for a generous sample of 20-hydroxyecdysone. Also, we acknowledge the technical assistance of Mr Wayne J. Snow.

Fisheries Research Board of Canada
Halifax Laboratory, Halifax, N.S.

MICHAEL W. GILGAN
M. ELIZABETH RETALLACK

Received for publication August 25, 1967.

REFERENCES

ANON. 1966. The Peet-Grady method. Soap Chem. Specialties, Blue Book, **1966**: 209–211.

GALBRAITH, M. N., AND D. H. S. HORN. 1966. An insect-moulting hormone from a plant. Chem. Commun., **1966**: 905.

KAPLANIS, J. N., MALCOLM J. THOMPSON, R. T. YAMAMOTO, W. E. ROBBINS, AND SPIRO J. LOULOUDES. 1966a. Ecdysones from the pupa of the tobacco hornworm, *Manduca sexta* (Johannson). Steroids, **8**: 605–623.

KAPLANIS, J. N., L. A. TABOR, MALCOLM J. THOMPSON, W. E. ROBBINS, AND T. J. SHORTINO. 1966b. Assay for ecdysone (molting hormone) activity using the house fly, *Musca domestica* L. Ibid., **8**: 625–631.

KOBAYASHI, M., K. NAKANISHI, AND M. KOREEDA. 1967. The moulting hormone activity of ponasterones on *Musca domestica* (Diptera) and *Bombyx mori* (Lepidoptera). Ibid., **9**: 529–536.

NAKANISHI, K., M. KOREEDA, S. SASAKI, M. L. CHANG, AND H. Y. HSU. 1966. Insect hormones. The structure of ponasterone A, an insect-moulting hormone from the leaves of *Podocarpus nakaii* Hay. Chem. Commun., **1966**: 915–917.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

1178. Shieh, H. S., and D. Spears. 1967. Utilization of choline or betaine for phospholipid synthesis in an aerobic marine microbe. Canadian J. Biochem., **45**: 1255–1261.

*1179. Margolis, L., and R. R. Parker. 1966. *Caligus japonicus* Gussev in Isakova-Keo, 1952, a synonym of *Caligus orientalis* Gussev, 1951 (Copepoda, Caligidae). Crustaceana, **10**(3): 311.

*1180. Dugal, L. C. 1966. Removal of fish tank stain with sulphur dioxide. Progressive Fish-Culturist, **28**(4): 231.

*1181. Arai, Mary Needler. 1965. The Ceriantharian nervous system. Am. Zool., **5**: 425–429.

1182. Medcof, J. C., and J. S. MacPhail. 1964. Fishing efficiency of clam hacks and mortalities incidental to fishing. Proc. Natl. Shellfish. Assoc., **55**: 53–72.

1183. Craigie, J. S., J. McLachlan, R. G. Ackman, and C. S. Tocher. 1967. Photosynthesis in algae. III. Distribution of soluble carbohydrates and dimethyl-β-propiothetin in marine unicellular chlorophyceae and prasinophyceae. Canadian J. Botany, **45**: 1327–1334.

1184. Ackman, R. G. 1967. Fatty acids of coho salmon fingerlings. J. Am. Oil Chemists' Soc., **44**(6): 372.

1185. Hodder, V. M. 1966. Trends in the haddock fishery of ICNAF Subarea 3. ICNAF Res. Bull. No. 3. p. 55–63.

1186. Brockerhoff, H., and R. J. Hoyle. 1967. Conversion of a dietary triglyceride into depot fat in fish and lobster. Canadian J. Biochem., **45**: 1365–1370.

1187. Donaldson, Edward M., and J. R. McBride. 1967. The effects of hypophysectomy in the rainbow trout *Salmo gairdneri* (Rich.) with special reference to the pituitary-interrenal axis. Gen. Comp. Endocrinol., **9**(1): 93–101.

1188. Mansfield, Arthur W. 1967. Distribution of the harbour seal, *Phoca vitulina* Linnaeus, in Canadian arctic waters. J. Mammal., **48**(2): 249–257.

1189. Ackman, R. G. 1967. Characteristics of the fatty acid composition and biochemistry of some fresh-water fish oils and lipids in comparison with marine oils and lipids. Comp. Biochem. Physiol., **22**: 907–922.

1190. Mansfield, Arthur W. 1967. The mammals of Sable Island. Canadian Field-Naturalist, **81**(1): 40–49.

1191. Bursa, A. S., and L. Johnson. 1967. Nannoplankton of marine origin from Great Bear Lake in the Northwest Territories of Canada. Nature, **214**(5087): 528–529.

Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies," composed of two parts. These are distributed to a selected mailing list. (Articles numbered 1020 to 1109 appeared in the Studies for 1966, Part 2).

***Indicates a "Titles only" paper which will not be included in the binding.**